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THE CONDOR

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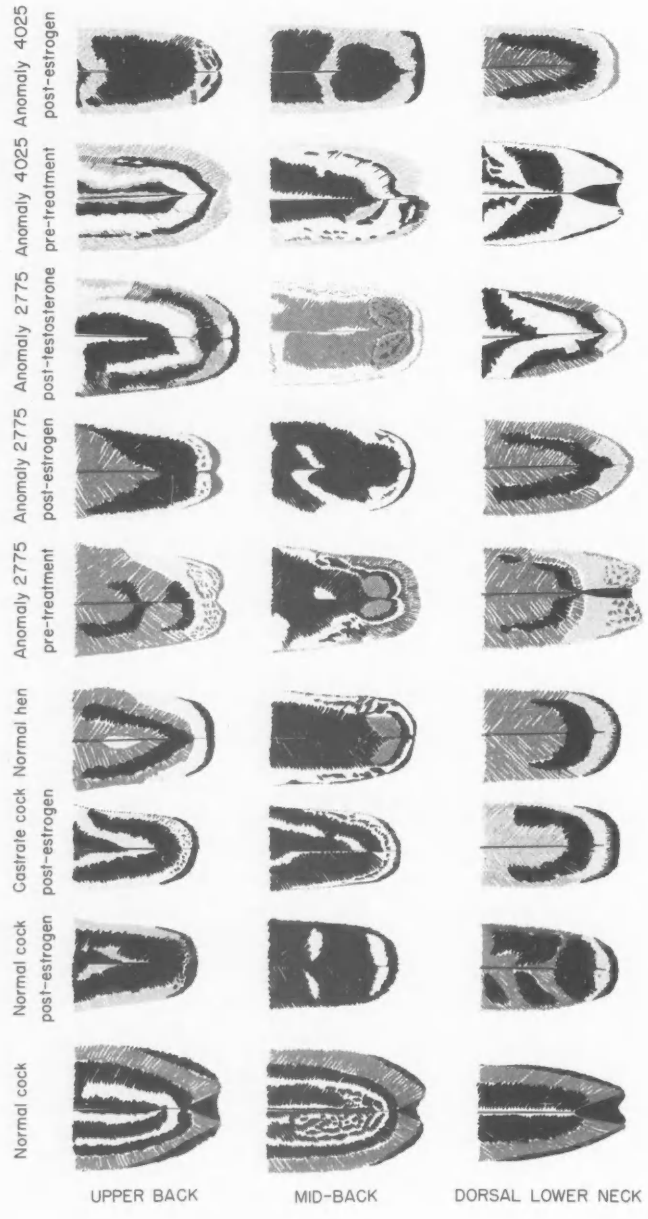

Feathers representative of certain tracts
in the Ring-necked Pheasant (*Phasianus colchicus*).
Anomaly 2775 was hen-colored; 4025 was cock-colored.

THE CONDOR

VOLUME 63 MARCH-APRIL, 1961 NUMBER 2

PLUMAGE DIFFERENTIATION OF NORMAL AND SEX-ANOMALOUS RING-NECKED PHEASANTS IN RESPONSE TO SYNTHETIC HORMONE IMPLANTS

By G. Victor Morejohn and Richard E. Genelly

Several investigators observed in the late 1920's that in some species of birds and mammals a number of secondary sexual characteristics, including color, seemed to be dependent on hormonal factors and not at all on the genetic sex of the individual. This led to the enunciation of a theory of "equipotentiality" which assumed that male and female tissues were identical in their reactions, particularly to the sex hormones (Lillie, 1927).

Allen and Doisy (1923) were the first to suspect that the ovarian follicular hormone was an estrogenic agent in mammals. Allen *et al.* later (1924) found that a similar substance could be extracted from the follicular liquor in the ovary of the domestic hen (*Gallus domesticus*). Much research, mostly with domestic animals, followed these discoveries. The domestic fowl served as a popular subject. Since the color and shape of feathers seemed more sensitive to hormonal changes during their growth than other secondary sexual characters, they were studied at great length. As a consequence of this it was found that castrated male chickens showed little or no changes in feather color or shape; yet ovariectomized females acquired male plumage. The injection of ovarian extracts, however, feminized both intact and castrate males as well as ovariectomized females. Much emphasis was placed on the theory of equipotentiality; but as experimental work expanded into other avian species, it was found that other relations obtained. The European House Sparrow, *Passer domesticus* (Keck, 1934) and the Brewer Blackbird, *Euphagus cyanocephalus* (Danforth and Price, 1935) did not respond to the estrogen theelin. The Black-headed Gull, *Larus ridibundus* (van Oordt and Junge, 1933) is ambisexual, responding to both male and female hormones and the African Weaver Finch (*Pyromelana franciscana*) has its plumage regulated by an hypophyseal hormone (Witschi, 1935, 1936). Obviously then, genetic as well as hormonal factors must interact to produce these different effects.

Previous studies of specific effects of genes in relation to their expressivity under estrogenic influence in Red Junglefowl, *Gallus gallus* (Morejohn, 1953, 1955) prompted the authors to investigate the nature of the difference in plumage between the sexes of Ring-necked Pheasants (*Phasianus colchicus*). Three "off-colored" birds were noticed among normal-appearing cocks and hens in an incoming group of pheasants used in other experiments. The three birds were caught, examined, and identified as sex anomalies of one type or another. Two of the birds were colored like hens, and one was cock-colored. A review of the literature revealed that several types of so-called "sex anomalies" had been reported in Ring-necks and other pheasants. Some were called hermaphrodites, others intersexes, and still others sex-inverts. From published descriptions and photomicrographs of internal organs it was difficult to decide in which of these categories to place the birds we had examined. Hermaphrodites were cock-feathered birds with spurs,

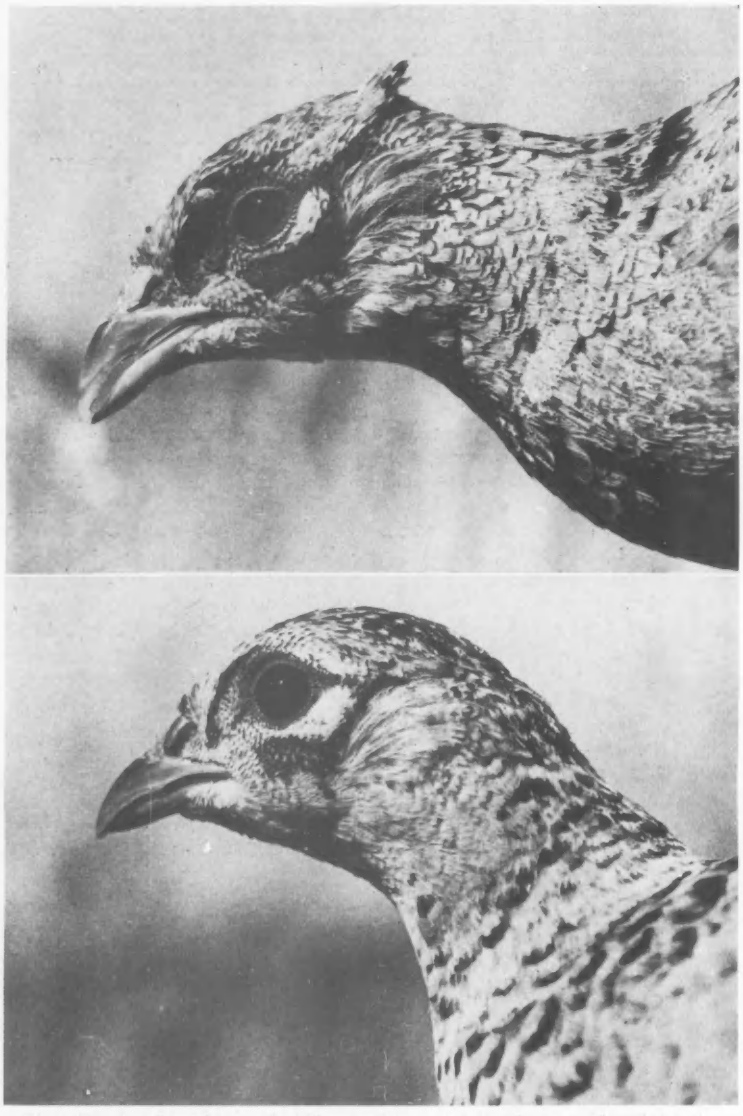

Fig. 1. Female-colored Ring-necked Pheasant intersex (top) and a normal hen (bottom). Note the presence of ear tufts, light-colored eyes, and large beak of the anomaly.

and these birds had both male and female organs. Intersexes were birds with supposed abnormal chromosomal complements which had mixed male and female feathers (sometimes called gynandromorphs), and sex-inverts were birds undergoing change from one sex to the other—usually female to male.

Previous investigators have given much thought and speculation to the origin and true nature of these sex anomalies but inadequate experimentation has been employed. Yarrell (1871–1885) was the first to report that a diseased state of the ovaries often induced production of male-type feathers in female Ring-necks in England. Gurney (1888) figured abnormal female organs from a cock-colored hen in his publication. Other investigators (Bond, 1914; Harrison, 1932; Rosen, 1948) have reported similar cases. Bissonnette (1940, 1941), however, reported birds that were essentially female-colored but possessed spurs, ear tufts, and gave the cock call. He also reported cock-colored hens with decidedly diseased ovaries. However, he believed both types were merely extremes of one phenomenon, that is, the ovaries became diseased, ovarian hormone secretion was curtailed, and the bird assumed cock plumage. This plumage is gradually lost as the bird's rudimentary right gonad begins to develop into an ovotestis or similar structure. During this time spur formation takes place and the bird gradually acquires a type of hen's plumage. In view of the work reported herein, this hypothesis seems untenable. It is believed that two separate conditions exist and that cock-feathered and hen-feathered individuals are not necessarily different stages of a deranged sexual progression.

Our three anomalous birds fit Bissonnette's description rather well. Two (fig. 1) were female-colored, possessed spurs, were large in size, had yellow irises and well developed ear tufts. The other (fig. 2) was cock-colored, had no spurs, was small with brown irises and no ear tufts. It can be seen, on the one hand, considering color and feather shape only, that two birds were female-like and one was cock-like; on the other hand, considering other so-called secondary sexual characteristics such as size, ear tufts, spurs, and iris color, two birds were male-like and one was female-like. This peculiar mixture of male and female characters will be dealt with later.

METHODS

The feather tracts of anomalous birds and normal males and females were compared. Examination of the cocks revealed that there were 22 distinct feathered areas on the normal bird. The normal hen was found to differ from the male in all of the recognized areas. Grossly, the differences (largely color and shape) between these feathered areas in cocks are clearly evident because of the difference in the color. In the hen, however, they may be distinguished only upon close examination. Feather samples were taken from each area as shown in figure 3 and mounted on sheets of cardboard. This was done for the normal cock and hen and for each of the anomalous birds. An evaluation of the individual feathers of the anomalous birds was made in relation to their degree of maleness or femaleness. Index values from zero to 4 were applied. Typical normal hen feathers were equated to zero; normal cock feathers were equated to 4. Intermediates were given the value of 2; those which tended to be more male-like the value of 3; and those which tended to be more female-like the value of 1 (table 1).

Instead of sacrificing the birds for studies of internal organs, it was decided to study their responses to subcutaneous implants of estrogen (diethylstilbestrol, 15 mgm. pellets) and androgen (testosterone propionate, 10 mgm. pellets). An experiment to determine responses to the hormones was set up as shown in table 2.

At the time of implantation of the hormone pellets approximately a dozen feathers were removed from each of the 22 different feather tracts. In this manner, the feathers that would subsequently replace those plucked would develop in a different hormonal

TABLE 1

A COMPARISON OF FEATHERS FROM VARIOUS PARTS OF THE BIRD

Feather samples were rated as follows: normal female, zero; mostly female, 1; intermediate (male-female), 2; mostly male, 3; and normal male, 4

Feather tracts	Normal hen	Anomalies 2775	2753	4025*	Normal cock
Dorsal head	0	0	0	1	4
Auricular	0	0	0	0	4
Dorsal lower neck	0	1	0	2	4
Lateral neck	0	0	0	4	4
Neck collar	0	0	0	4	4
Ventral lower neck	0	1	2	3	4
Upper back	0	1	1	2	4
Mid-back	0	1	1	1	4
Lower back	0	1	1	1	4
Upper rump	0	0	0	1	4
Lower rump	0	0	0	1	4
Anterior breast	0	2	1	3	4
Mid-breast	0	3	3	3	4
Posterior breast	0	0	1	3	4
Humeral	0	1	1	1	4
Lesser coverts	0	0	0	0	4
Median coverts	0	0	0	2	4
Greater coverts	0	0	0	2	4
Lower femoral	0	1	1	2	4
Upper femoral	0	1	1	1	4
Upper tail coverts	0	1	1	3	4
Caudal	0	1	1	3	4
Rating totals:	0	15	15	42	92

* Cock-colored anomaly.

background and the effect of the implanted hormone would be seen readily on the newly emerging feathers. The effects of the hormones lasted about six or seven weeks, and most feathers had grown about two-thirds of their full length in this time. Little chance of error occurred in plucking out the experimental feathers since much of the basal feather shaft was still growing and was bluish and soft. The feathers grown under the

TABLE 2

EXPERIMENTAL PROCEDURE USED TO DETERMINE RESPONSES TO HORMONES IN NORMAL AND SEX-ANOMALOUS RING-NECKED PHEASANTS

Sex type	Experiment I Diethylstilbestrol response	Experiment II Testosterone response
1. Normal intact ♂ (control)	.....	.....
2. Normal ♀ (control)	.....	.....
3. Normal ♀	No	No
4. Normal intact ♂	Yes	No
5. Normal castrate ♂ (control)	.....	.....
6. Normal castrate ♂	Yes	Yes
7. Anomaly 4025 (cock-colored)	Yes	No
8. Anomaly 2775 (hen-colored)	Yes	Yes
9. Anomaly 2758 (hen-colored) (control)	.....	.....

influence of the hormone were then compared with the feathers which had been plucked from the same site previous to implantation.

RESULTS

Results of estrogen implantation.—The effects of estrogen were evident in all birds except the normal hen (no. 3 in table 2). Contrary to expectation, however, males did not assume typical female feathers. The feathers were dull and brownish, and the pattern of pigment distribution was not at all similar to that found in the normal female. Moreover, to complicate the matter further, the castrated males developed some feathers

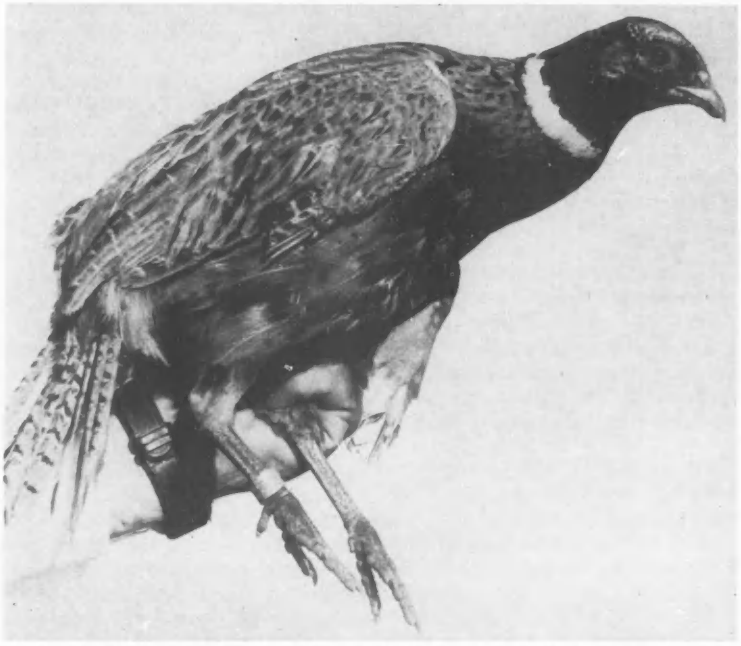

Fig. 2. Cock-colored female of the Ring-necked Pheasant. This bird had a diseased ovary and was believed to be a genetic female. Disregarding color compare the morphological features of the head with the normal female in figure 1 (bottom).

that differed from those developed by the intact males. These differences were most clearly evident in the dorsal lower neck, upper back and mid-back feather tracts. The lateral neck, neck collar, lower back, upper rump and lower rump were similar in both. The other tracts showed only minor differences between intact and castrated males.

All regenerated feathers of the hen-colored anomaly closely resembled the normal female type with the exception of the mid-back, lower back, upper rump and lower rump. These feathers approximated those produced in the same areas under estrogen influence by castrated and intact males.

The cock-colored anomaly produced feathers under the influence of estrogen similar to those of the hen-colored anomaly. The feathers of the back and rump, however, were

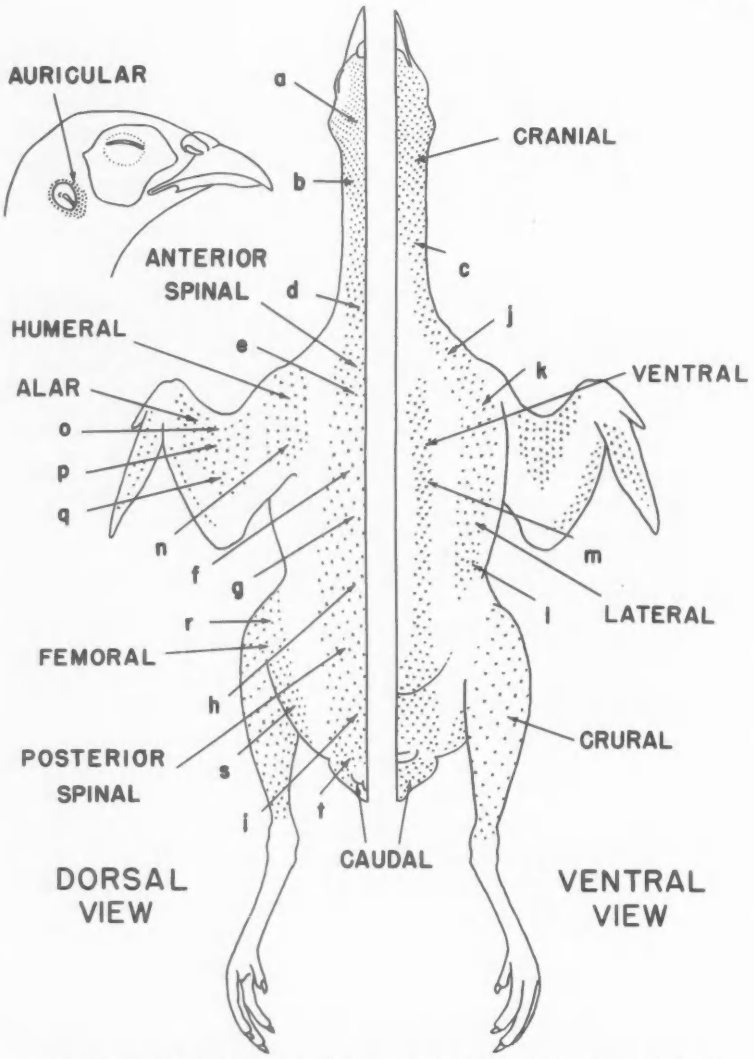

Fig. 3. Diagram of dorsal and ventral views of the major feather tracts of *Phasianus colchicus*. Feathers from specific areas in the feather tracts were employed. The areas, indicated by letters, are as follows: CRANIAL TRACT, (a) dorsal, (b) lateral neck, (c) neck collar; SPINAL TRACT, (d) dorsal lower neck, (e) upper back, (f) mid-back, (g) lower back, (h) upper rump, (i) lower rump; LATERAL TRACT, (j) ventral lower neck, (k) anterior breast, (l) posterior breast; VENTRAL TRACT, (m) mid-breast; HUMERAL TRACT, (n) posterior; ALAR TRACT, (o) lesser coverts, (p) median coverts, (q) greater coverts; FEMORAL TRACT, (r) lower femoral, (s) upper femoral; CAUDAL TRACT, (t) upper tail coverts. The drawing at the upper left demonstrates position of the auricular tract.

more nearly like those of the normal female than the feathers produced by the other birds. Other pre-treatment feather samples were more female-like than those produced post-treatment.

Results of testosterone implantation.—All remains of implanted pellets were removed from the skin of the neck on the experimental birds to rid them of any lingering effects of estrogen. The birds were then replucked in several sites. Males were examined two weeks later and the new emerging feathers were still hen-like. Four weeks after removal of the pellets the same feathers were re-examined and their bases were seen to be cock-colored. The effects of estrogen were obviously gone. At this time, the birds were re-implanted with testosterone and replucked.

Testosterone produced no response at all on the feathers of the normal female. In fact, the hen given testosterone had been laying and continued to do so. Noticeable redness and increased size of face wattles, however, were evident. No plumage change was seen in the intact male, but he became very active and had greatly expanded face wattles and erect ear tufts. This male actually dominated the normal control male. The castrated male behaved similarly to the normal male, but he was by no means as active and had smaller facial wattles.

The feathers on the hen-colored anomaly were affected by testosterone and somewhat resembled the feathers on the cock-colored anomaly. The facial wattles became very large, and the ear tufts were prominent and carried erect. In spite of its overall female-like color, it strutted about the pen and behaved like a normal male. The only striking feather changes seen in this bird were in the region of the neck collar, lateral neck and upper back. The feathers in these regions were masculinized: the neck became greenish and the collar feathers became white. The feathers of the back and rump, however, responded in an unexpected way. They became more female-like than those in the same area previous to any hormone treatment. The feathers in the other parts of the body remained somewhat feminine in character and showed only slight masculinization. Regenerating feathers of the cock-colored anomaly under testosterone treatment were no different than pre-treatment feathers.

Sexual status of the anomalies.—At the end of the experiments the anomalies were sacrificed and their gonads examined. The cock-colored anomaly proved to be a female with a diseased ovary. Histological sections revealed a non-functional ovary with no follicles present, but numerous small, cellular circular areas resembling degenerate follicles were present beneath the germinal epithelium. Black pigment granules were distributed throughout the organ. Intermingled throughout the tissue of the ovary were cords of adrenal-like tissue. The oviduct appeared normal.

Both hen-colored anomalies possessed an ovary-like structure, a testis, vasa deferentia, and an oviduct. In section, the ovary was much like the one described above, and the testis had many irregularly shaped seminiferous tubules without lumina, the cells of which were undergoing mitosis. Many tubules of the epididymis were also in evidence. The left adrenal was absent. Abnormal sexual conditions such as these have been observed by Crew (1923), Domm (1927), Fell (1923), and Lillie (1927).

DISCUSSION

Consideration must first be given to the responses to hormones in the group of normal birds studied. The normal intact male reacted somewhat differently to estrogen than the normal castrate, and both produced feathers mostly unlike those of the normal female (see frontispiece). This response to estrogen is unlike that which is usually found in the domestic chicken, such as the brown leghorn and other breeds which have the same plumage pattern as found in the Red Junglefowl. In these birds, as in most other

phasianids which differ sexually in the color and shape of feathers, there is no evidence of sex-linked inheritance of plumage differences between males and females. The difference in sexually dichromatic breeds of fowl seems to be the direct effect of the hormone estrogen in females. In other domestic breeds of fowl and many semi-domestic birds, mutations affecting feather form and color are well known (Hutt, 1949). Genes affecting these characteristics are located in autosomes as well as in the sex chromosomes. The dominant sex-linked gene which determines barring of feathers in some domestic chickens, for example, has a different effect on males and females depending upon whether the individual has one or two genes for barring. Since the gene is located in the sex chromosome, females can have usually only one because they are hemizygous. Males have two sex chromosomes and when homozygous for this gene usually have a lighter appearance than heterozygous males since a double "dose" of the gene has a greater inhibitory effect on the deposition of melanin which forms the dark bars. Barring, however, is not known to be greatly affected by gonadal hormones. It seems likely that the major sexual differences in feathers in the Ring-necked Pheasant are produced in two ways: (1) by autosomal genes having different expressivity under hormonal influence, and (2) by sex-linked genes having different expressivity dependent upon whether they are single genes (as in the hemizygous female) or paired genes (as in the male). A single or double dose of the gene would give different responses to the hormone. Apparently, the feather tracts of the back and rump in this pheasant are governed by sex-linked genes since there is such a pronounced effect evidenced in males under the influence of estrogen (see frontispiece). The other regions are probably governed by autosomal genes for they approach more nearly the female feather pattern and shape under the effects of estrogen. The feathers of the dorsal lower neck, upper back, mid-back, and humerals seem to respond differently to estrogen in the absence of testosterone. The presence of testosterone seems to inhibit in these feather tracts the complete action of estrogen in intact males. In the absence of testosterone, estrogen is able to exert its feminizing effects more clearly, thus resulting in feathers resembling closely the typical female. It seems likely, therefore, that the feather tracts of the back and rump (upper back, mid-back, lower back, upper rump, and lower rump) are governed by genes in the sex-chromosomes, and that the dorsal lower neck, upper back, and mid-back tracts are much more sensitive to the action of estrogen in the absence of testosterone. Feather samples representing responses to hormones are shown in the frontispiece.

Our interpretation of sex-linked genes controlling plumage differentiation is also supported by the work of Smith and Thomas (1913), especially their observations in regard to the intergeneric hybrids which they produced. They found that sterile hybrid female pheasants, which were comparable to birds with non-functional ovaries (as in the cock-colored anomaly), often showed cock-colored feathers in certain tracts. These male-like feathers were similar to the types found in the male parent. In other words, the F_1 hemizygous female received its sex chromosome from the male of one genus and the genes governing certain feather tracts in that genus exerted their effects on the sterile hybrid female plumage. Obviously, sex-linked genes controlling plumage differentiation are found in other pheasants as well. Danforth's (1937) skin transplantation experiments on *Phasianus* provide the following support of the hypothesis of dosage effects on plumage: (1) Female skin of the rump transplanted to the rump of the male host produced feathers which were not completely masculinized. Iridescent green color was absent and feather form was not perfect. This is in accord with the hypothesis that hemizygous female skin would not show complete dosage effects of testosterone. (2) Male hosts carrying female skin and given estrogen produced typical female feathers in the graft, whereas adjacent feathers were incompletely feminized.

The responses given by the anomalies are not as easily explained. In fact, some results were exactly opposite of what was expected. The anomalies would not be expected to respond simply, so that at best a complex response seemed likely. The hen-colored anomaly or intersex may have possessed an abnormal chromosomal condition initially. There is no proof of this. An interpretation of responses to hormone implants was difficult since the bird had elements of both testis and ovary and perhaps low titers of both gonadal hormones. It responded, as might be expected, in a feminine way to estrogen in both the upper back and dorsal lower neck tracts. In fact, the resemblance to the castrated male given estrogen was marked (see frontispiece). The mid-back tract, however, which closely approximated the normal female before treatment, responded to estrogen much as did the castrated male given estrogen. The dorsal lower neck behaved likewise. The response of the upper back tract to testosterone, as one might predict, resembled the normal male. The mid-back tract reacted to testosterone as it should have reacted to estrogen and vice versa. This may be an example of the so-called exceptional cases of masculinization by estrogens and feminization by androgens. Generally all other tracts showed responses to testosterone similar to that which obtained in the dorsal lower neck tract—some masculinization together with intricate patterns not uniformly found in the tracts themselves. The cock-colored anomaly, however, gave responses similar to that which might be observed in an ovariectomized hen. This bird, as a matter of fact, may be considered an example of a gonadless female. That is, the plumage she carried may well represent the resultant plumage produced in an ovariectomized normal female. The incomplete feminization of plumage may be due to an unknown substance or to exogenous hormones. The differences in response found in the upper back tracts as compared to the males given estrogen may, perhaps, be accounted for as a dosage effect, since this bird was probably a genetic female. The responses to testosterone were virtually identical to pre-treatment plumage, or it may be said that there was no response to testosterone in regenerating feathers in this bird.

SUMMARY

The responses to implantation of the hormones, synthetic diethylstilbestrol and testosterone propionate, in Ring-necked Pheasants demonstrated that plumage differentiation of both sexes is dependent upon genetic as well as hormonal factors, and that the genetic nature of this differentiation is associated with autosomal genes as well as genes in the sex chromosomes. The latter genes exert their effects through their intermediaries, hormones, and the differences in plumage between the sexes is one of genetic dosage. The three anomalies that were studied indicated an aberrant intersexual condition in one type, the hen-colored form, probably genetic in nature, and in the other type, the cock-colored form, a genetic hen with a diseased ovary.

LITERATURE CITED

Allen, E., and Doisy, E. A.
1923. An ovarian hormone. Preliminary report on its localization, extraction and partial purification, and action in test animals. Jour. Amer. Med. Assn., 81:819–821.
Allen, E., Whitsett, J. W., Hardy, J. W., and Kneibert, F. L.
1924. The follicular hormone of the hen ovary. Proc. Soc. Exper. Biol. and Med., 21:500–503.
Bissonnette, T. H.
1940. The "mule" pheasant. Sex-invert or intersex? Jour. Heredity, 31:83–88.
1941. The "mule" pheasant. Proc. Amer. Philos. Soc., 85:49–70.

Bond, C. J.
1914. On a case of unilateral development of secondary male characters in a pheasant, with remarks on the influence of hormones on the production of secondary sex characters. Jour. Genetics, 3:205–216.
Crew, F. A. E.
1923. Studies in intersexuality.—II. Sex-reversal in the fowl. Proc. Roy. Soc. London, 95: 256–278.
Danforth, C. H.
1937. Artificial gynandromorphism and plumage in *Phasianus*. Jour. Genetics, 34:497–506.
Danforth, C. H., and Price, J. B.
1935. Failure of theelin and thyroxin to affect plumage and eye-color of the blackbird. Proc. Soc. Exper. Biol. and Med., 32:675–678.
Domm, L. V.
1927. New experiments on ovariotomy and the problem of sex inversion in the fowl. Jour. Exper. Zool., 48:31–174.
Fell, H. B.
1923. Histological studies on the gonads of the fowl. I.—The histological basis of sex reversal. Brit. Jour. Exper. Biol., 1:97–130.
Gurney, J. H.
1888. On the occasional assumption of the male plumage by female birds. Ibis, ser. 5, 6:226–230.
Harrison, J. M.
1932. A series of nineteen pheasants (*Phasianus colchicus* L.) presenting anomalous secondary sexual characters in association with changes in the ovaries. Proc. Zool. Soc. London, 1932:193–203.
Hutt, F. B.
1949. Genetics of the fowl (McGraw-Hill Book Co., New York).
Keck, W. N.
1934. The control of the secondary sex characters in the English sparrow, *Passer domesticus* (Linnaeus). Jour. Exper. Zool., 67:315–347.
Lillie, F. R.
1927. The present status of the problem of 'sex inversion' in the hen. Jour. Exper. Zool., 48: 175–196.
Morejohn, G. V.
1953. A gene for yellowish-white down in the red junglefowl. Jour. Heredity, 44:46–52.
1955. Plumage color allelism in the red junglefowl (*Gallus gallus*) and related domestic forms. Genetics, 40:519–530.
Rosen, M. N.
1948. Hermaphroditism in Chinese ring-necked pheasant. Calif. Fish and Game, 34:135–136.
Smith, G., and Thomas, H.
1913. On sterile and hybrid pheasants. Jour. Genetics, 3:39–52.
van Oordt, G. J., and Junge, G. C. A.
1933. The influence of the testis hormone on the development of ambosexual characters in the blackheaded gull (*Larus ridibundus*). Acta. Brev. Neerl., 3:15–17.
Witschi, E.
1935. Seasonal sex characters in birds and their hormonal control. Wilson Bull., 47:177–188.
1936. Effect of gonadotropic and oestrogenic hormones on regenerating feathers of weaver finches (*Pyromelana franciscana*). Proc. Soc. Exper. Biol. and Med., 35:484–489.
Yarrell, W.
1871–1885. A history of British birds. 4th ed., vol. III (John Van Voorst, London).

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VOICE AND SOCIAL BEHAVIOR OF THE CHUKAR PARTRIDGE

By Allen W. Stokes

The Chukar Partridge (*Alectoris graeca*) is difficult to study in the rugged country in which it occurs in the United States. Life history studies of the Chukar in Nevada (Christensen, 1954), Washington (Galbreath and Moreland, 1953), and Utah (Phelps, 1954) have dealt mostly with habitat and food requirements but only slightly with calls and social behavior. Hume and Marshall (1880), in what is the best description of the bird in its native range, have little to say about calls or displays. Since so many calls of the Chukar are soft and infrequent, they are best studied under penned conditions. Goodwin's study (1953) of the closely related Red-legged Partridge (*Alectoris rufa*) has been a great help. The white chin flanked by the black V, the conspicuous dark and white vertical bars on the flanks, and the chestnut tail feathers covered with gray upper tail coverts are conspicuous plumage characters prominent in the display of both species. Many of their calls are similar in quality and the situation in which they occur. Studies of the brown leghorn chicken by Wood-Gush (1954, 1956) have been especially valuable for their descriptions and analyses of galliform behavior. Wherever possible I have used the same terminology as the aforementioned authors in describing calls and behavior patterns.

This paper presents observations on the behavior of the adult Chukar Partridge both in the wild and in captivity. This account is largely descriptive with only tentative conclusions about causation and function of behavior. For a quantitative analysis of the motivation of calls and display the reader is referred to a forthcoming paper "Agonistic and Sexual Behaviour in the Chukar Partridge" (Stokes, in press).

This study was made from 1955 through 1960. In 1955 I kept three males and five females in a pen with wire sides and top measuring 40×60 feet from January through May. The floor of this pen was bare ground during winter, but it had moderate ground cover in spring. In 1956 I used 12 males and 12 females. Three males and three females were kept in the same outdoor pen as in 1955 to observe display and pair formation. The remainder were separated as to sex and kept apart from the birds in the pen. From time to time these birds were placed singly in the pen to observe the reaction of the penned birds to newcomers. In 1957 I held 16 birds in three outdoor pens measuring 30×60 feet with emphasis on nesting behavior. In 1960 most observations were of birds kept in isolation except during paired encounters between birds of the same or opposite sex. These birds were exposed to 14 hours of artificial light daily from January 15 until the end of observation in May. Paired observations of these birds began in March at a time when sexual and aggressive behavior was increasing rapidly. In addition to the caged birds, I observed Chukar Partridges in the wild in northern Utah for about 40 hours.

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CALLS

The calls of the Chukar are numerous and variable. I have divided calls into those associated with alarm, social contact, and agonistic or sexual situations. Those occurring in the same situation as in the Red-legged Partridge I have marked with an asterisk.

Alarm Calls

*The ground alarm call.**—A person's first experience with Chukars in the wild is likely to be in the fall as a covey of birds flushes wildly a few yards in front of the hunter. The birds separate in long, curving downhill flights. As they burst from the ground the first call is a loud piercing squeal, followed by a series of *whitoo whitoo* calls gradually subsiding as the birds disappear out of range. Birds leaving their roost on some rocky outcrop in the faint light of dawn fly downhill with these same calls, as do birds evicted from an aggressor's territory in spring. In the pens a bird when suddenly attacked or chased by another bird may give the same short squeal and *whitoo* call. Birds held in my hand gave the squeal and *whitoo* calls as I waved them up and down. Hence one cause of the call is the appearance of a sudden or unfamiliar stimulus on the ground; another is eviction by an aggressor. But I do not know what elicits the call during flights from roosts or on other occasions when there is no apparent disturbance. This call seems similar in nature to the cackling of a Ring-necked Pheasant (*Phasianus colchicus*) as it leaves its roost or is startled by the hunter.

*Hawk-alarm note.**—A large bird or airplane flying overhead generally elicits a short, guttural *kerrrr*. It is evenly pitched and given with little mouth movement, but it is audible for perhaps 100 feet. If the disturbance is not too close, the bird will crouch on the spot and turn its head sideways to get the best possible view. The call may be repeated several times by the first bird to see the disturbance and also by other birds in the pen even though they cannot see the danger. More sudden or closer sources of danger sometimes send the entire flock of Chukars flying or running hastily to cover.

When first placed in new surroundings, the birds were alarmed at many disturbances such as hawks or eagles soaring overhead, the sudden disappearance of the sun behind a cloud, or low-flying airplanes. Later the birds might give a single *errrrk* with scarcely a break in their activity. Black-billed Magpies (*Pica pica*), Crows (*Corvus brachyrhynchos*) and even Starlings (*Sturnus vulgaris*) would at times cause alarm, but this probably hinged on the suddenness of approach and the silhouette they presented to the Chukars. These same birds when perched immediately above the pens caused no alarm. This was true even for a Sparrow Hawk (*Falco sparverius*) that seconds before perching had caused the entire flock to crouch.

After the disturbance had subsided, the birds gave soft, broken rally calls. More often they would give the contentment call (see beyond).

*"On-guard" call.**—This is a low-pitched, undulating *kwerr* given when a hawk continues soaring overhead. The birds give it while frozen and looking up at the hawk either from cover or out in the open. It may be given intermittently for several minutes or until the hawk has disappeared. The call is difficult to locate and has the characteristics of a well-adapted alarm note described by Marler (1955), that is, it is easy to recognize but difficult to locate.

Contact Calls

*Food call.**—Single birds feeding at the hopper or scratching in the litter frequently gave a slow *took*. This is sharp and emphatic with a clear pause between each note. I have heard this call in the wild as a pair of partridges fed slowly across a grassy opening. I believe it serves to keep the birds aware of others in the group. Among chicks the call is a turkey-like *turk*. Birds that discover a new or novel source of food will call excitedly a rapid *tu-tu-tu-tu*. I could always elicit this call by depriving my birds of food for a few hours or by introducing earthworms to the pen. The adults called their young to food using the same note.

*"All's well" call.**—A loafing or feeding bird will at times give a soft plaintive *coo-oor*, rising in pitch on the second syllable. Birds give it when there is no apparent strife or tension from outside sources. The call frequently signifies the end of a period of alarm from the air. In the Red-legged Partridge, Goodwin (1953) believes this is the call of a paired male given while standing at ease. The same may be true of Chukars, for I have recorded it only from males in the breeding season. I have heard it, however, from two males kept isolated for over a week from the single hen with which they had been kept. They were, moreover, never paired with her and were dominated by a third male before separation. The fact that only the male gives this call, and only in the breeding season, suggests that this call may be sexual rather than purely social.

Agonistic and Sexual Calls

Numerous calls occur only or chiefly in the breeding season. These may be agonistic or sexual in nature.

*The rally call.**—This is the most common call of Chukars and the one from which the species derives its common name. At low intensities the call is *chuck, chuck, chuck*, given slowly and with definite breaks between each call. As the intensity of the calling rises, it changes to *per-chuck, per-chuck* with accent on the second syllable, and it is given at faster tempo. This in turn gives way to *chukar-chukar-chukar* with accent on the first syllable. At highest intensity, and usually highest volume, the call becomes a three-syllable *chuckara-chuckara-chuckara*. A bird may go from one form to another quickly, and I have not been able to distinguish different functions or causation in the various forms of this call. At highest intensity a single call may last 20 seconds with as many as three calls a minute. The female gives the same call but much less often, at least during the breeding and brood season.

A bird may give the rally call while walking or running, but typically it gives the call while standing still. At low intensity the bill is scarcely opened. Otherwise, the bill is opened wide, cheek and throat feathers puffed out, and the head held high and somewhat forward. With each call the tail makes synchronized, slight, up and down movements. The neck feathers, especially those on the nape, are fluffed, creating an obvious hump. Likewise the feathers from the rump up to the middle of the back are fluffed to create a hump in this region (fig. 1a).

Chukars generally give their rally call from the ground. At times they call from low perches available to them, and the wild Chukars near my pens would even call from high fence posts. But this habit is not nearly as common as among Bobwhite Quail (*Colinus virginianus*).

I have heard the rally call in fall after the birds of a covey had been dispersed by hunting, but I have not studied it outside the breeding season. It appears that the rally call becomes more frequent and intense with the advent of the breeding season. The diurnal variation is like the variation in song birds. First calls begin about 45 minutes before sunrise and are at a peak at sunrise. Their frequency falls off rapidly within an hour after sunrise and stays low until about an hour before sunset. Calls may persist until about 45 minutes after sunset, becoming shorter, softer and less frequent as darkness falls. The evening peak is somewhat less than the morning peak.

Outside of the sunrise and sunset periods, the rally call may be given in a number of other situations. In captivity when two males are confined in a small pen together, only the dominant cock will give the rally call. Birds in pens always directed their calls to birds outside the pen. During 1957 there were several wild Chukars outside of the pen. A sudden outburst of the rally call was always a sign of a wild bird approaching.

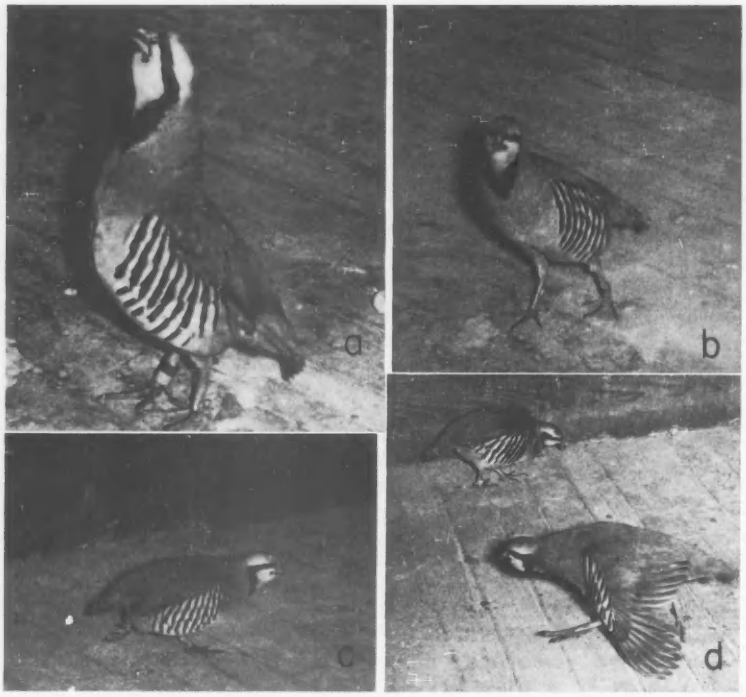

Fig. 1. Behavior of Chukar Partridge (*Alectoris graeca*). a, Rally calling by male, showing swollen throat of dominant bird. b, Head tilt; male is displaying to unseen bird at right; note barred flank feathers pulled up over wing. c, Running threat. d, Waltzing; wing of waltzing male is scraping the ground; female in rear shows no signs of fear.

Rally calls were especially loud and persistent on the several occasions when a bird had escaped from the pen and was wandering about outside. One year a group of Chukars was penned outdoors some 200 yards away and out of sight of my experimental birds. There was always a strong period of rally calling by these birds as daylight came.

Whenever a predator has scattered a covey and made it take shelter for any length of time, the first cautious movements of the birds as they leave shelter are accompanied by rally calls—somewhat quiet at first, then louder and louder. One July evening I watched a flock of 25 birds move up a steep canyon slope to roost. Halfway up, a Golden Eagle (*Aquila chrysaëtos*) swooped over and forced the birds to cover. After 10 minutes of absolute quiet the birds slowly started out. First one, then several, gave the rally call. Within two minutes the cliffs were ringing with their calls. Within another few minutes the flock had reassembled and had begun working its way up the slope.

Throughout the day in spring, bursts of rally calling may occur. Typically these occurred whenever two males met aggressively. Following a chase and withdrawal of the males to their own areas one or both might call repeatedly. This in turn often started other males calling. During these bursts of calling a male seldom moved but usually

remained conspicuous in some opening or on a raised piece of ground. In these encounters it seemed to be always the males that were calling.

It appears that the rally call has three functions. First, because of its loudness, it announces the location of the calling bird. This may serve to repel intruding males, for in spring the call is certainly aggressive in nature. Second, it may be sexual in function, serving to attract females to the male as in the "advertising" song of many other birds. However, since pair formation tends to occur within the covey, this sexual function of the rally call may not exist. Unlike some quail (Stoddard, 1931; Genelly, 1955) the male Chukar continues to call long after he has paired. But persistent callers heard in mid-July were lone males and may well have been unpaired. Third, the call occurs after a covey has been scattered. In this situation it appears to serve as a means of aiding scattered birds in rejoining the covey, and it is given by females as well as males throughout the year. Rally calling in this last situation appears to come under an entirely different motivational situation than calls during the breeding season. In this respect it differs from the "advertising" songs of the Ring-necked Pheasant and quail, which appear to be entirely aggressive male behavior. However, there has been no critical study of rally calling outside the breeding season. It may be that the difference between the Chukar Partridge and other gallinaceous birds is less real than apparent.

*Steam-engine call.**—A male in breeding season may give a harsh *chak-chak-chak* call, sometimes lasting for five minutes on end; at other times, just a few isolated calls may be given. Walpole-Bond (1938) first used this name in connection with the Red-legged Partridge; but it applies equally well to the Chukar. At a distance one could easily mistake this mechanical call for some ancient-vintage steam engine of a ferry boat. The male gives it with head held high and body erect. At high intensity the body feathers are somewhat fluffed, especially those of nape and neck, as in the rally call.

The call occurs in situations that suggest a conflict between aggression and escape. Thus two males in adjacent pens may display vigorously toward each other with head tilted and circling for several minutes. The dominant male tries to peck the other through the wire. Finally it moves off several feet and starts the steam-engine call. In general whenever a dominant male is prevented from getting at another, he will give this call. A dominant wild male used to fly into one of my pens regularly and consort with a female and several males. Every time I chased it out of the pen it would fly off 50 yards to a clearing and start calling. Here the wild male's aggressive behavior was thwarted by my presence. One captive male used to dominate the wild male. Every time the wild male approached the pen, the captive male would give the steam-engine call. Here, too, the more aggressive bird was thwarted by being unable to fly out of the pen to attack the wild outsider.

In the wild, however, it appears to be the subordinate male that gives the steam-engine call while the dominant male may give the rally call. Thus I have observed a male give repeated rally calls over a 10-minute period in a small clearing on a knoll. The calls were long and loud suggesting highly aggressive motivation. Another male was skirting the clearing and keeping out of sight and somewhat lower on the knoll. It gave repeated steam-engine calls but no rally calls. Likewise birds that fly down from their roost giving the *whitoo* escape call may immediately begin the steam-engine call on landing. Although too dark to determine, it seems likely that the dominant male in a roosting covey chases the subordinate males shortly after waking. The latter "steam-engine" where they alight lower down; the dominant males give the rally call from the roosting site.

Birds in the same pen rarely give the steam-engine call. An exception is when a paired male has been forced away from his mate by a dominant male. Then the submissive

male will retreat to an uncontested area and give short bursts of this call, but usually these short bursts are quieter than normal. Perhaps when males can actually come together either aggressiveness or fear will dominate, resulting in attack or retreat rather than unresolved conflict.

Goodwin (1953) states of the Red-legged Partridge, "This is primarily the 'song' of the male in the breeding season . . . . It seems functionally parallel with the song of male passerine birds, as an advertisement of the (?territory-holding) male's whereabouts." In Chukars, at least, this call does not begin to have the important function of true song. It is given under far too limited conditions. Instead it appears definitely to be linked with strong conflict in motivation between attack and escape.

Either sex may give a quieter and much shorter form of the steam-engine call when disturbed. A bird cornered in the pen would always give this call; the more closely pressed the bird, the louder and more harsh the call; at its highest intensity the call closely resembles the steam-engine call. This is not surprising, for being cornered must also represent conflict between fear and aggression.

When I placed a young Marsh Hawk (*Circus cyaneus*) in a pen with two adult male Chukars, they gave a loud steam-engine call for several minutes while they walked back and forth some 12 feet away from the hawk. Interspersed with the steam-engine call was the "contact" note. This situation again placed the birds in a position of balance between attack and retreat with retreat dominating. Seven-week-old chicks gave a mild form of *chak-chak* on approaching the hawk, but they seemed less alarmed by it than the adults.

Another time male RY had been dominant over male R in a pen for several days. Then a third male that was somewhat dominant over RY was placed in this pen. RY no longer attempted to display toward the new male. Instead he went off some 15 feet and gave the steam-engine call. This was a situation in which RY had met his equal and no longer was able to attack, so he "vented his spleen" with the steam-engine call during his thwarted aggression.

"Squee" call.—When two males are placed together, the dominant male, once it has established its social position, will frequently give a characteristic, excited call. This is highly variable consisting of mouse-like squeaks (*squee*), shrill peeps, and *whitoo*-like calls. These are all given rapidly with little or no break between one call and another. This call frequently changes into the rally call and back again. It appears to share the same motivation with the rally call, but presumably at lower intensity. Dominant males appear to be the only birds giving the call. Whenever I separated a dominant male from the rest of the flock so that he could hear and perhaps see the others, he would peck vigorously at the barrier and give this *squee* call. Birds within the same pen never gave this call once the peck order was established. Hence the call occurs when a male is in conflict between attack and escape with the aggressive tendency somewhat stronger than the escape tendency.

Waltzing calls.—In between waltzing bouts while the male is standing laterally to the male or female in tense, erect position, he will often give a call of several seconds duration much like the aerial alarm call. It is either an *errrrrrr* or *errrrk*, the latter being shorter in length.

Submissive squeal.—A bird being chased or suddenly attacked may give a rasping squeal lasting one or two seconds with bill held wide open. A hen may squeal when being chased by a particularly aggressive hen or by an aggressive cock during his attempts to copulate. Captive hens that had laid over a dozen eggs and had developed signs of broodiness resisted attempts of males to copulate and squealed frequently. Submissive

cocks also squealed when being dominated by a cock. If a bird was actually grabbed by the nape, it was likely to continue squealing until it had broken loose from the attacking bird. The merest move in the direction of the subordinate bird was often enough to elicit a squeal. This sort of squeal was most common during the breeding season, a time when aggressiveness between birds was at a peak. Although the squeal was given with extreme submission, there was no evidence that it had appeasement value. Dominant birds continued their attacks during and after squeals without letup.

The calls given during agonistic behavior are thus good indicators of the motivation of the calling birds. The rally call is an indicator of strongest dominance and aggression; the *squee* call somewhat less. The steam-engine call comes with high intensity conflict between aggression and escape where the calling bird is somewhat subordinate to the rival. The waltzing call is given by a bird that is somewhat dominant, especially over a female. Here the conflict is probably between aggression, escape, and sexual tendencies. Finally, the squeal is given by distinctly subordinate birds with strong escape tendencies.

Sexual Calls

Another group of calls occurs only in the breeding season and seems to function in bringing the pair together for copulation and orientation to the nest. I have designated these as sexual calls.

*Tidbitting call.**—During the tidbitting display (see courtship behavior beyond) the male utters a rapid *tu-tu-tu-tu-tu*, which becomes more rapid and higher pitched as tidbitting continues. A single round of calling may last over a minute. This call may be identical to the food call, but it is more varied in pitch and is longer and louder. This may be merely a difference of intensity.

Pitoo.—The male gives this call in the presence of the female as a single call or repeated every few seconds. At such times he is relaxed and moving about freely, never in display. But typically the call precedes a bout of tidbitting or may be injected among the tidbitting calls.

*Nest-ceremony call.**—This is a soft continuous *churr*, rising and falling erratically in pitch. It is very similar to the food call. Either sex may give this while exploring for nest sites or turning in a nest scrape.

*Copulation-intention call.**—When a male intends to copulate with a hen he stands erect several feet behind her, then he runs directly up to her. During this stage he invariably announces his intention to copulate with a deep-throated rattle, *uh-uh-uh-uh*. In rhythm and quality it also closely resembles the tidbitting call. But it is steady in pitch and volume and lasts for only two to three seconds, stopping the second the male mounts the female. At the height of the breeding season, when dominant males were strongly motivated sexually, I have heard them give this copulation-intention call before running up behind submissive cocks and grabbing them. Hence the call may be elicited by any crouching bird that is facing away from the male involved, so long as he is strongly motivated.

AGONISTIC BEHAVIOR

During fall and winter Chukar Partridges tolerate each other and spend much of their time in coveys. Birds roost and loaf in tight groups, and even while feeding they remain close together. However, with advent of spring, intolerance increases and males may become strongly aggressive toward others. Aggressiveness in birds is known to increase with increased testosterone output in spring (Davis and Domm, 1943). The range in behavior from attack at one extreme and escape at the other is known as agonistic

behavior. Among Chukars it becomes most frequent during the breeding season. Most intense behavior occurred when I introduced two males to each other for the first time.

Aggressive Behavior

Head tilt.—The most common display is the "head tilt." In this the male tilts his head away from the bird being intimidated. At the same time the aggressive bird turns sideways to expose his barred flank feathers to the utmost. These flank feathers may be brought well up over the tightly folded wings (fig. 1b). The feathers of neck and chin are fluffed out to such an extent that the neck appears to be half again as large as that of a female or subdued male. During a head tilt the male also stands erect and stiff. This low-intensity display is almost a necessary precursor to more intense displays. A male may make this threat toward a strange male on first encounter or toward other males as a means of forcing a subordinate male away from courting a female. Once the dominance of a male has been established, the head tilt proves an effective deterrent to subordinate males. One afternoon I observed a wild male attempt to put its head through the fence of the pen to feed. The dominant male among my captive birds, about 30 feet away at the far end of the pen, had only to cock his head to make the outsider withdraw, even though there was a tight fence between them. The head tilt is the least aggressive of threat displays and the first to appear in the spring.

Circling.—A more intense form of display occurs when the aggressive male makes a half circle about another bird, at the same time holding his head tilted toward the outside of the circle. Circling is performed by the bird destined to become the dominant one in a paired encounter. The dominant bird circles if the initial head tilts fail to make the second bird submissive. Where birds are fairly evenly matched, mutual circling may last for five minutes before the second bird escapes or crouches submissively. At lower intensity, circling may be a slow walk or a mere step or two. Circling is also frequent when a second male is courting a female. The aggressive male uses this display to force the subordinate courting male away from the hen. Should the second male persist in remaining beside the hen, the aggressive male will make a series of very rapid half circles between the two birds. Like a well-trained cow pony, the aggressor will keep cutting the second male off from the hen no matter how fast the other male may be.

When two males of equal dominance first meet in early spring, there will be mutual head tilting as the two birds stand several feet apart in stiff stance. Later they may run slowly side by side. An aggressive bird will never stand head on to another bird but always so that his flank feathers show. There may be periods in which no antagonism is demonstrated between nearly equal males. But after half an hour the dominance of one is established. Later in the season, as birds become more aggressive, an encounter seldom lasts more than two minutes before dominance is established.

Running threat.—If a male sights another male intruding on his territory, he will challenge the intruder by running straight toward him in a special manner found only in this situation. In running, the back and tail are horizontal and the head straight in front but somewhat lower than the back (fig. 1c). On stopping, the bird stands up stiffly and gives a head tilt, turning sideways as he does so. After a few seconds he will resume his run toward the intruder. He may make half a dozen such short spurts before coming close enough to the intruder to begin more intense displays. I have seen males in the wild run 100 feet or more in this manner to repel an intruder. On returning to his mate the male may run in the same way.

Waltzing.—Sometimes after several minutes of circling, a male may go into what appears to be a still more intense form of display—the waltz (figs. 1d, 2a). This appears

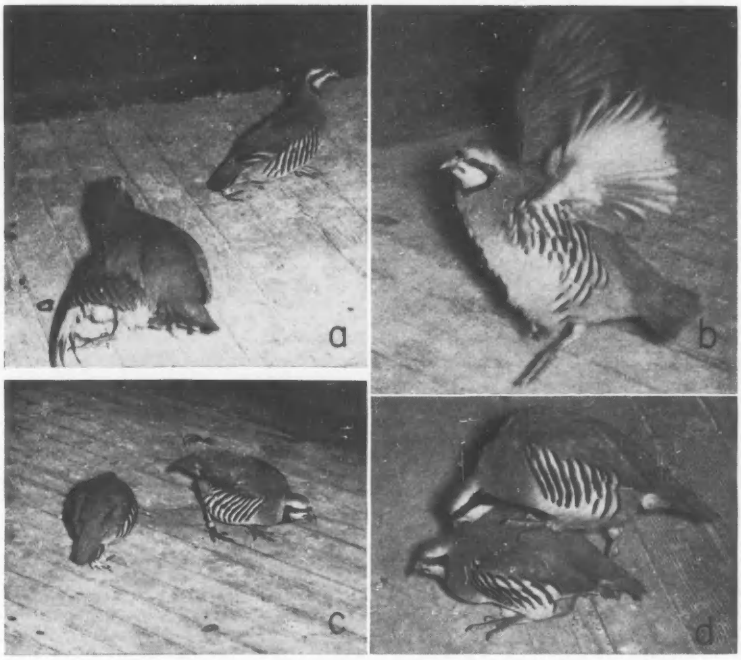

Fig. 2. Behavior of Chukar Partridge. a, Waltzing; the tremendous vigor of the waltz is shown by the tilt of the male's body and the wing extended to the floor; the female is escaping; note her raised wing tips, constricted throat, as compared with the male's, and strongly flexed legs while running. b, Wing flapping by submissive bird. c, Tidbitting by male to the right; female has joined male and the male has turned away just prior to moving away in high-stepping. d, Copulation, wings of female partly raised; male is preparing to grab the female by the nape.

comparable to that described in domestic fowl (Davis and Domm, 1943). In waltzing the body is held horizontally and head low as in threat running. Most of the body feathers, especially those of the flanks and rump, are raised during running. The head may be tilted somewhat outward as in circling. Almost always the outer wing is lowered so that the tips of the primaries scrape the ground. This wing may be lifted at an angle of about 45 degrees from the body. The inner wing is never lowered and tends to be almost entirely concealed by the fluffed flank feathers. The male may make half a dozen complete circles about the bird to which he is displaying. However, should the second bird be under a bush or in a corner, the displaying male may make figure-eight runs away from and back toward the second bird. Between waltzes the male will stand erect and laterally to the second bird. Body feathers will become normal and the extended wing withdrawn. At this time the male may give the waltzing calls. In captivity waltzing may last for five or six minutes before the aggression of the male wanes and he resorts to other behavior such as tidbitting and copulation.

When there are three or more males in the same pen with hens, one can invariably observe the following behavior: One male will dominate all other males at will but he

seldom threatens them. He does little or no courting of females. The second-ranking male will dominate all other males and will display frequently toward them with head tilt and circling. He will also court one or more hens intensively. Either of these actions will invariably elicit threats from the dominant male. He will cut between the courting male and the female, waltz vigorously, and make the second-ranking male desist.

Tidbitting.—This ritualized form of feeding accompanied by characteristic calls occurs mostly during male-female encounters and is described under "Courtship Behavior." Between males it occurs at low levels of aggressiveness and usually after the initial circling and head tilting have abated.

Attack.—A male will rarely attack another bird without some preliminary display. Attacks are usually preceded by waltzing or circling which become steadily more direct, rather than lateral, in their direction. Finally the dominant male will make a direct rush and grab the other bird by back or nape feathers, often to the point of breaking the skin of the defensive bird. Closely balanced birds may fight for several minutes before the conflict is resolved, but this is unusual. Attack, unlike copulation, is generally from the side rather than the rear.

Calls of the dominant bird.—During 15-minute paired encounters of birds in indoor pens, the dominant male always gave the *squee* call of aggression and the rally call. These were most common after the relative dominance of the two birds was settled. The submissive bird never gave either of these calls.

Submissive Behavior

During paired encounters between males one can quickly determine by behavior which bird is destined to be submissive. Submissive birds start wing flapping almost at once after facing an aggressive male (fig. 2b). In wing flapping the bird stands straight on its feet, gives a vigorous flap of its wings and actually rises slightly off the ground. During flapping all body feathers including those of the crown are strongly fluffed, and the bird usually faces somewhat away from the aggressor. Rarely does the aggressor flap. Following flapping, and at other times as well, the submissive male may ruffle his feathers. Another sign of submissiveness is turning away from the aggressor. Under more intense aggression the submissive bird begins running away. First indicator of escape is the raising of the wings, so that the tips of the primaries meet above the bird's back. This is in contrast to the behavior of birds in non-agonistic situations, where the primary tips rest well below the back. Submissive birds run with legs well bent and body horizontal. They hold the head far back on the shoulders and squeal. Chases may persist for several minutes. Eventually the submissive bird crouches in some sheltered position. The deep motionless crouch is the very opposite of aggressive behavior and tends to conceal both barred flanks and white throat patch that stand out on an aggressive bird. This submissive behavior serves to stop further aggression for the most part.

The contrast between dominant and submissive birds is shown in table 1 which summarizes behavior of paired encounters between males. These males had been kept isolated except during encounters. They were first tested at the stage in their reproductive cycle when they were courting females actively. There was a clear-cut distinction between behavior of dominant and submissive birds. Once dominance was established, there were no reversals in social rank on subsequent encounters. I have not studied establishment of the peck order outside of the breeding season. However, in 1955 three males and three females were placed together in early January. I observed occasional gentle pecks at other birds but no overt display. I suspect that the peck order takes much longer to be established in winter than during the breeding season.

Males behave aggressively toward females as well as males. This is not surprising since the sexes are alike in appearance. In the domestic fowl Wood-Gush (1960) has found that males isolated from females during the breeding season behave very aggressively toward females when first introduced to them. This is true of Chukars also. Typically the male attempted to copulate with the hen within 30 seconds of introduction to her, and often was successful. This was followed immediately by five to ten minutes of

TABLE 1

BEHAVIOR OF DOMINANT AND SUBMISSIVE MALE CHUKAR PARTRIDGES IN 44 PAIRED ENCOUNTERS FROM MARCH TO MAY, 1960

Behavior	Dominant males		Submissive males	
	Number of occurrences	Per cent of dominant males displaying	Number of occurrences	Per cent of submissive males displaying
Attack	227	50	1	2
Waltzing	39	16	0	0
Squee call	372	55	7	5
Rally call	397	57	10	7
Circling	596	82	6	9
Lateral stance	188	68	12	9
Steam-engine call	8	9	3	2
Tidbitting	41	25	14	13
Bill wiping	19	16	55	25
Feather ruffling	57	68	152	93
Wing flapping	35	43	267	98
Avoidance	3	7	856	89
Squealing	0	0	939	55

intense waltzing accompanied by aggressive calls. Only after this release of aggressive behavior would the male then resort to appeasing behavior leading to further copulations. Females showed the same avoiding and appeasing behavior as submissive males, but they might be attacked just as vigorously as males.

Females rarely acted very aggressively toward other females. Usually aggressiveness consisted merely of one female running toward the other. This frequently caused the submissive hen to move a few feet to the rear of the dominant hen. Circling and waltzing were infrequent among females. Females tended to be most aggressive after pair formation while repelling females intruding into a territory.

COURTSHIP BEHAVIOR

Courtship among animals may serve four functions: orientation of male and female, persuasion, synchronization, and reproductive isolation (Tinbergen, 1953). Courtship behavior was originally thought to be solely a sexual phenomenon. We now know that this behavior stems from a conflict in the simultaneous tendencies for male and female to act sexually, aggressively, and submissively toward the partner. This conflict of tendencies has brought about the evolution and ritualization of courtship behavior (Tinbergen, 1953; Hinde, 1953). The behavior of Chukars follows these principles of causation and function of courtship.

Courtship among Chukars typically has the following pattern. The male will at first act aggressively toward the female. Circling, head tilting, and waltzing may occupy five to ten minutes. The female meanwhile continues with her activity of the moment—preening, feeding, or dusting. Only when the male is overly aggressive may she avoid,

squeal, and even take cover. The intensity and frequency of these displays gradually wane and the male tends to perform farther and farther away from the female. Eventually the male seemingly loses interest in the female and begins to feed or preen. But soon he may move off some five to 20 feet from the female and begin a display well known among domestic fowl as "tidbitting" (Davis and Domm, 1943; Wood-Gush, 1956). In this the male makes incipient pecks toward the ground, especially at conspicuous objects such as stones, feathers, earthworms, or even food particles (fig. 2c). True pecking and picking up of objects follows, associated with the tidbitting call. The male holds his legs half bent, body sloped downward from tail to head, wings held tightly to the body, crown lowered, and tail either straight back or somewhat bent under. The bill is pointed downward but seldom comes closer to the ground than a half-inch during mock pecking.

Early in the season the female makes no response to these calls. But later she may instantly break off her own activity, run to the male and begin pecking at the same or nearby objects. This lasts for a few seconds, until the male suddenly stands erect and moves off in a stiff-legged step called "high-stepping" in domestic fowl (Wood-Gush, 1956). In high-stepping the male is more erect than in any other stance, with breast almost vertical. He bends his legs only slightly in running and holds wings and feathers in normal position. The male almost always moves around to the rear of the female and again tidbits. Tidbitting, then, appears to have strong appeasement value. Hens that had just previously been strongly evasive of a waltzing cock soon approached the tidbitting male. Another indication of the appeasing value of the tidbitting display was that copulation was most likely to follow a series of tidbitting displays, but it rarely occurred during waltzing.

Precopulatory behavior is highly stereotyped. It begins with the female facing directly away from the male and crouching deeply with head forward and below the level of the back. The male stands still and erect about three to ten feet behind the female for a brief moment. He then gives the precopulation rattle and at once "high-steps" rapidly toward her with breast and flank feathers well fluffed. The female intensifies her crouch and raises her folded wings to horizontal position and holds them there throughout copulation. The male stops calling as he places his foot solidly in the middle of her back, grabs vigorously at her nape, and mounts (fig. 2d). He crouches on her back, wings outstretched and extended so that they come completely over her flanks. He presses his tail downward until it touches the ground, the female's being tilted to one side. Copulation lasts about three seconds, after which the male dismounts and "high-steps" off several feet. The female may continue her crouch for several seconds, then gets up and ruffles her feathers vigorously. Rarely does a second copulation immediately follow.

The female may crouch while feeding or dusting. This often releases copulatory behavior in the male. In this situation the female tends to rise or take a single step as she hears the male give his precopulation rattle. This suffices to stop the male from further approach. Rape, however, may occur when males have been separated from females over a long period of time. They may then be so aggressive that they grab the female from the side and then mount her vigorously despite her efforts to escape. In outdoor pens rape occurred especially late in the breeding season when the females were well along in egg laying but the males were still highly motivated sexually.

Ordinarily the necessary stimulus to release copulation behavior in the male is the sight of a female facing away from him and fully crouched. The female may initiate this orientation by turning away from the male. Or the male may move around until he is

behind her. This "rear approach" has likewise been observed in domestic fowl (Skard, 1937; Wood-Gush, 1956).

The female may disrupt the male's copulatory intentions by merely turning so that the male is no longer behind her. The male may make a series of these "rear approaches" without ever inducing crouching in the female. I agree with Wood-Gush (1956) that the sexual tendency is dominant in the "rear approach." But the escape tendency is apparently sufficiently strong so that the male breaks off his copulation attempt unless the female crouches and orients properly.

Another element of courtship is the "nest ceremony." Usually the male initiates this by entering a clump of vegetation. He then crouches, usually holds his tail almost vertical and spread so that the rusty tail feathers are conspicuous, and turns slowly in nest-scraping motions. He may also move sticks and grass with his bill in a drawing motion. At highest intensity the bird will hold its wings slightly outstretched and quiver both wings and tail rapidly. All this time he gives the nest-ceremony call. When both male and female are at the site together, the ceremony is most intense. One bird performs in the nest while the other stands close by. Birds change places every 30 seconds or so. This exchange may go on for several minutes at a time and may be repeated on and off all day.

Observations of birds on the wooden floor of the indoor pen gave some insight into the nature of the releasing stimuli for the nest ceremony. At first, birds never performed the nest ceremony, but they might make motions of scratching, turning and pulling objects into the "nest." But when I placed a clump of weeds in one corner of the room, both male and female performed the nest ceremony within a few minutes. A week later the birds performed the ceremony in any darkened corner of the room. Hence the releasing stimuli presumably became less precise as the internal motivation of the bird increased. However, at no time was the nest ceremony indoors as intense as that outdoors.

In the first three years of the study I first observed the nest ceremony on April 1, March 17, and March 16. The latest I saw it was on May 17. It preceded egg laying by a full three weeks. Highest-intensity display occurred after birds were paired. At such times the male's nest ceremony call often attracted the female to the nest. But the male rarely responded to the female's initial nest calls. I never observed nest display once egg laying began.

Wood-Gush (1954) describes a similar ceremony in domestic fowl under the name "cornering." His roosters' behavior was similar to tidbitting and dust bathing and included a call very similar to that heard in tidbitting. But since his birds were in bare pens, I suspect a corner was a substitute nest site and the behavior he observed was in fact ceremonial nest building.

Since the male Chukar shares in raising the brood, this display may serve a valuable function in keeping the male closely oriented to the female during egg laying and incubation. In addition, in various members of the genus *Alectoris*, including Chukars, the male may incubate and hatch the first clutch (Goodwin, 1953). Hence this display may be still more important in orienting the male to the future nest of eggs.

A female may also perform ritualized nest building when away from the nest. She will pick up sticks or grass and throw them over her shoulder one after another. The first time I observed this behavior the hen had been in a nest form idly tossing stalks over her shoulder for several minutes. She then moved out to the edge of the nest clump and continued this throwing, gradually working her way out until six feet from the nest.

The first occurrence in spring of the various forms of aggressive and sexual behavior followed their order of increasing intensity. Thus males in outdoor pens began tilting their heads in threat the last week of January. Circling began on February 9, and waltz-

ing on February 22. Pair formation began as early as March 9, with nest calling on March 15. Earliest copulation was witnessed on March 20 and egg laying on April 10.

Pair Formation

Pair formation was a subtle act. Certainly the male's initial circling observed in late February and early March in outdoor pens was not directed toward his eventual mate. Once paired, the pair appeared to prefer a particular area of the pen, for that day at least. The pair was particularly intolerant of other females. Whether a paired male was intolerant of other males depended upon his social rank. Later in the breeding season a male might pair with a hen within 24 hours after she had been placed in the pen.

I had most success in getting birds to pair in 1955 when the three males and three females were together steadily from late December. In 1956 and 1957 I never observed a definite pair formation. Perhaps this was due to fairly frequent shuffling of birds. This was in contrast to observations by Goodwin (1953) that birds that were too familiar with each other did not pair readily.

The history of male GW in 1955 illustrates some of the behavior during pair formation. GW was lowest in peck rank of three males in the pen. He was chased frequently and pecked occasionally during early spring before and during courtship. GW started circling female R in early February, but never paired with her then. Then on March 2, GW appeared paired with female RB. They paced restlessly back and forth along one fence steadily for an entire day and kept separated from the other four birds in the pen. A week later, however, GW was definitely paired with female R, his original partner. They remained in one corner and side of the pen almost steadily. Meanwhile RB, the jilted female, kept trying to approach GW. However, female R kept chasing her away with short lunges. During the next two days the two females seemed about evenly balanced. They paced back and forth along one fence with male GW between them, so actual contact between the two hens was minimal. After that, however, RB gave up attempts to stay with GW.

In the meantime, male GW actively herded his mate R into the corner of the pen every time she strayed too far. Several days later, however, R was able to move about more. In doing so she frequently moved into an area used by G, the dominant male. When GW attempted to keep by R's side, male G almost invariably drove GW away with head tilt or actual circling or herding. Very similar behavior occurred with the second-ranking male. Hence the ability of a male to stay with his mate hinged upon his social rank. In the wild, one would ordinarily expect paired birds to withdraw from the covey and escape the intolerance or domination of higher ranking birds.

Although GW was lowest in rank of the three males, he succeeded in having four mates over a two-month span, his previous ones dying from accident or disease. On the other hand, the dominant male G did not acquire a mate until April 15, a full five weeks after GW was paired. G performed a minimum of courtship display and finally paired with the bottom-ranking female. Hence the strong aggression of dominant males may inhibit their ability to appease females, resulting in their being slower to pair.

Although paired birds tended to remain in a particular area of the pen for a day or more at a time and were intolerant of intruding birds, I do not think this was strictly a defended territory. Some pairs would remain in one area for several hours, then suddenly move to the other side of the pen, remain there for several more hours, and finally move on to still another area. So no pair held to a single area for more than a day or two. My limited observations in the wild, however, indicate that Chukars have well-defined territories that they defend vigorously.

Causation of Courtship Behavior

One is immediately struck by how much of the dominant bird's display is a lateral presentation: circling, waltzing, and the stationary lateral erect posture. Indeed it is only during the running threat from a distance and in actual attack that one bird approaches another directly during agonistic encounters. These lateral displays are enhanced by the conspicuous barred flank feathers. The fact that attack rarely occurs without preliminary lateral display of some kind strongly suggests that even the most aggressive bird hesitates to attack. Circling of the opponent represents a compromise between approach and retreat, the displaying bird being in a position to move in or away at any instant, which in fact he frequently does. The first attacks by an aggressor represent a gradual transition from lateral circling or waltzing to diagonal approach and final direct attack. This is the same whether the dominant male is displaying to another male or to a female.

Tidbitting almost never occurs during waltzing sessions. Instead it tends to occur first as the aggressiveness of the male has waned and his waltzes stop. During tidbitting the male shows some fear of the female for he tends to avoid the female shortly after she runs up to him. Yet the male is sexually motivated for he often copulates with the female soon after he shifts from waltzing to tidbitting. Hence the tidbitting display appears to be the resultant of low aggressive and moderately high escape and sexual tendencies.

It is striking that the copulation, tidbitting, and nest-ceremony calls all bear a close resemblance to the aerial alarm call. It may well be that these have all evolved from the more primitive alarm call and retain an element of alarm as a causal factor in each instance. We are presently observing the ontogeny of these calls and hope to determine their relationships through sound spectrograms.

The male ordinarily attempts to copulate only when the female crouches, the least aggressive position she can take. In addition the male breaks off his approach to the female should she make a slight move. Hence it seems likely that the male is in conflict between sexual and escape tendencies.

The female shows fewer signs of conflict in her behavior. This is understandable because she shows very little aggressiveness toward other birds. Thus hens kept in isolation from cocks during the peak of the mating season were usually ready to crouch the minute a cock was placed in the same pen. Once this initial copulation had occurred, the hen was strongly evasive of the male for some time before she was again ready to solicit copulation. It appears that her sexual motivation was high when first placed with the male. But after copulation the sex tendency dropped and the escape tendency dominated her behavior. Whether a hen crouches or avoids seems to be the result of a rather sensitive balance between sexual and escape tendencies.

Courtship behavior, therefore, is the resultant of the conflicting tendencies to attack, escape, or act sexually. In early stages aggression is dominant and courtship consists chiefly of the more aggressive elements of circling, waltzing, and rally calling. As the sexual tendency increases and aggression wanes these forms give way to tidbitting, nest ceremony, and accompanying calls that serve to appease the female, eventually ending in copulation.

SUMMARY

The Chukar Partridge was studied for four years, observations in the wild augmenting those of captives. Fourteen calls of adults were classified according to their association with alarm, social contact, agonistic, or sexual situations. Most common was the

rally call. During the breeding season it was an aggressive call, serving to announce a dominant male and to repel intruders. Rally calls were at a peak at sunrise and sunset. Throughout the year the rally call also serves to reunite scattered birds.

Several calls depended upon the bird's aggressiveness. As the aggressiveness of a bird toward an opponent decreased, one heard in descending order the following calls: rally, *squee*, waltzing, steam-engine, and submissive squeal. Sexual calls included the tidbitting, nest-ceremony, and copulation-intention calls.

When two strange males met during the breeding season, their relative dominance was settled within a few minutes. Aggressive elements of behavior included: circling, head tilt, lateral stance, waltzing, running threat, and attack, as well as the aggressive calls listed above. Submissive birds never called except for the submissive squeal. They flapped their wings and ruffled their body feathers frequently, avoided the aggressor, sleeked all body feathers, and when escaping raised their wing tips over the back and held the head back on the shoulders while running. Females showed little aggressiveness toward other birds.

When a male was first placed with a female, courtship began with a period of waltzing and other aggressive display. It was followed by tidbitting and then copulation. As the breeding season advanced, the nest ceremony became important in maintaining the pair bond.

Pair formation was slow in early spring, but it became much more rapid later. The dominant male in a group did far less courting than the second-ranking male. He also paired later than less aggressive males.

Courtship displays appeared to be the resultant of the relative and absolute strengths of the attack, escape, and sexual tendencies of the male, and to a lesser extent those of the female.

LITERATURE CITED

Christensen, G. C.
1954. The chukar partridge in Nevada. Nev. Fish and Game Comm., Biol. Bull. No. 1.

Davis, D. E., and Domm, L. V.
1943. The influence of hormones on the sexual behavior of domestic fowl. *In* Essays in Biology (Univ. Calif. Press), pp. 171–181.

Galbreath, D. S., and Moreland, R.
1953. The chukar partridge in Washington. Wash. State Game Dept., Biol. Bull. No. 11.

Genelly, R. E.
1955. Annual cycle in a population of California quail. Condor, 57:263–285.

Goodwin, D.
1953. Observations on voice and behaviour of the red-legged partridge *Alectoris rufa*. Ibis, 95:581–614.

Hinde, R. A.
1953. The conflict between drives in the courtship and copulation of the chaffinch. Behaviour, 5:1–31.

Hume, A. O., and Marshall, C. H. T.
1880. The game birds of India, Burmah, and Ceylon. Vol. II (published by the authors, Calcutta).

Marler, P.
1955. Characteristics of some animal calls. Nature, 176:6.

Phelps, J. E.
1954. The adaptability of the Turkish chukar partridge (*Alectoris graeca* Meisner) in central Utah. Utah State Dept. Fish and Game, Inf. Bull. No. 15.

Skard, A. G.
1937. Studies in the psychology of needs. Acta Psychol., 2:175–232.

Stoddard, H. L.
1931. The bobwhite quail (Charles Scribner's Sons, New York).
Stokes, A. W.
1961. Agonistic and sexual behaviour in the chukar partridge. Anim. Behav., *in press*.
Tinbergen, N.
1951. The study of instinct (Clarendon Press, Oxford).
1953. Social behaviour in animals, with special reference to vertebrates (Wiley and Sons, Inc., New York).
Walpole-Bond, J.
1938. A history of Sussex birds (H. F. and G. Witherby, London).
Wood-Gush, D. G. M.
1954. The courtship of the brown leghorn cock. Brit. Jour. Anim. Behav., 2:95–102.
1956. The agonistic and courtship behaviour of the brown leghorn cock. Brit. Jour. Anim. Behav., 4:133–142.
1960. A study of sex drive of two strains of cockerels through three generations. Anim. Behav., 8:43–53.

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THE BIOENERGETICS OF VERNAL PREMIGRATORY FAT DEPOSITION IN THE WHITE-CROWNED SPARROW

By James R. King

In seeking to identify the external factors and internal mechanisms which initiate and characterize avian migration, it appears that one of the more profitable avenues of approach is through an analysis of the physiology of premigratory fat deposition. It has been emphasized by many investigators (Wolfson, 1942; de Bont, 1947; Farner, 1955; Helms and Drury, 1960) that this deposition is characteristic of many small migratory species, that it does not occur in sedentary species, and that it is one of the earliest and most prominent signs of the physiological preparation for migration. In an analysis of the component mechanisms of premigratory fat deposition there are several obvious preliminary questions which delimit the approaches to orderly field observation and meaningful experimental design: (1) What are the quantitative and temporal characteristics of fat deposition under natural conditions? (2) What are the sources of energy which underlie intensive fat deposition? (3) What are the environmental timers, if any, which initiate deposition and the dissipation of the surplus reserves? (4) What neuro-endocrine changes and alterations in intermediary metabolism are involved?

In an earlier paper concerning the first of these questions (King and Farner, 1959), we have quantitatively analyzed the phases of vernal premigratory fattening in wild White-crowned Sparrows of the race *Zonotrichia leucophrys gambelii* and compared the pattern with that of captive members of this same race. It was emphasized that quantitative differences between wild and captive birds were relatively minor and that temporal differences were not detectable. Because of this similarity, it was concluded that captive birds could legitimately be used in experimental analysis of the physiology of premigratory fattening. The investigations to be described below relate to question 2 and, in part, to question 3 as they apply to captive *Zonotrichia leucophrys gambelii*.

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MATERIALS AND METHODS

The birds employed in this investigation were obtained from overwintering populations in the Snake River Canyon of southeastern Washington. This population represents the northernmost limit of the regular winter range of *Z. l. gambelii*. This is a strongly migratory race of the White-crowned Sparrow which breeds in the boreal zones of northwestern North America and overwinters in a broad area of the West extending from southern Washington to Utah, Nevada, Oregon, California, and northern México. The northern limit of the major wintering range is separated from the southern limit of the breeding range by about 200 miles, although the majority of the population migrates much greater distances (up to 3300 miles; Blanchard and Erickson, 1949).

From mid-March to early June of 1955 and 1956, six male *Z. l. gambelii* were studied under outdoor conditions at Pullman, Washington. The birds used in 1955 had been captured between October, 1954, and February, 1955, and had been held in outdoor aviaries until 10 days before the beginning of the study, when they were placed in the metabolism-activity cages described beyond. The six males used in the spring of 1956

had been captured in January of that year and in October of 1955. They were also given a 10-day period of acclimation to the small cages.

The outdoor laboratory was a walled enclosure on a roof four floors above the street level. The metabolism-activity cages were placed on a shelf with an east exposure and protected from rain and snow by an overhanging roof. Except for this necessary protection of the apparatus from precipitation, and for a somewhat reduced wind velocity, the birds were subjected to normal variations in weather conditions and photoperiod. Climatic conditions at Pullman do not differ markedly from conditions on the nearby wintering grounds in the Snake River Canyon. Mean temperatures in January for these two areas are −2.6°C. and 0.8°C., respectively.

Measurement of energy intake.—For the study of energy income, birds were confined individually to Hendryx breeding cages (23×36×28 cm.) from which the floors had been removed. Each cage was set in an aluminum pan 12.5 cm. in depth which prevented the loss of spilled food and excreta. Aluminum tubing was used for perches in order to facilitate the quantitative recovery of droppings, and an aluminum partition was inserted across the lower half of the cage beneath the central perch. The procedure for measuring energy intake was similar in principle to that of Kendeigh (1949), Seibert (1949), and Davis (1955). A quantity of food weighed to the nearest 0.05 gm. was supplied daily in a tared glass hopper. The food consisted of a chick-starter mash prepared by the Department of Poultry Science at the Washington State University. This is a nutritionally adequate ration consisting of 74.7 per cent carbohydrate, 20.7 per cent protein, 3.1 per cent fat, and 1.5 per cent ash, and it also includes mineral and vitamin additives. For use in these observations the mash was passed through a corn grinder to reduce the size of particulate components (mostly cracked corn). This eliminated the possibility of selective feeding and facilitated the preparation of a homogeneous mixture. The moisture content of the ration was determined each week by drying to constant weight at 98°C.

At prescribed intervals (4 to 7 days, as noted beyond), the metabolism pans were changed. All food and excreta adhering to the bird's feet, the cage and its accessories were collected and placed in the pan. The spilled food and excreta in the pan were then mechanically separated by multiple screenings and hand picking. The separated materials were dried to constant weight at 98°C. It was not possible by this procedure to separate completely the excreta and spilled food, but with sufficient care the mutual contamination was reduced to about 100 to 200 mg. in an average collection. Because the caloric values of food and excreta are not very different (*ca.* 4.5 kcal./gm. and *ca.* 3.5 kcal./gm., respectively) this contamination is largely cancelled. It is estimated that the maximum experimental error was about three per cent.

The energy content of the food and excreta was determined by routine oxygen-bomb calorimetry. The acceptable limit of error between duplicate samples was set at 0.4 per cent of the mean value. The energy content of three different batches of chick-starter used in this investigation was 4.439, 4.540, and 4.552 kcal./gm. dry weight. There was no detectable selective feeding by the birds. Residual food gave the same combustion values in several tests as the food supplied to the cages.

The computation of energy income was accomplished as follows: The dry weight of the food supplied was computed from the measured moisture content of the ration. The dry weight of the residual food was determined directly by drying to constant weight. The difference between the food supplied and the residual food was multiplied by the energy content as determined by bomb calorimetry, giving the gross energy income of the bird for the period. Subtracting from this the energy content of the excreta for the

same period (excretory energy), also determined by bomb calorimetry, yields the metabolizable energy, which is the energy actually available to the bird for maintenance, storage, and work (minus the indeterminate fraction lost in the specific dynamic effect of the ration and in fermentation, if any, in the gut). The utilization coefficient is obtained from the equation: metabolizable energy/gross energy × 100. It denotes the percentage of the gross energy income which is actually assimilated by the bird.

In these investigations it was very desirable to obtain an estimate of the energy expended in maintenance functions and muscular work. In order to estimate this energy quantity, which will be called the catabolized energy, it is necessary to know the caloric equivalent of change in body weight during periods of fat deposition and depletion. In man, this factor is estimated to be between 6 kcal./gm. of weight change (Keys and Brozek, 1953) and 7.8 kcal./gm. (Wishnofsky, 1958). In the White-crowned Sparrow during the premigratory period the water content of the subcutaneous fat varies between means of 13 and 37 per cent (McGreal and Farner, 1956). The caloric equivalent of weight change in this species will therefore lie between about 6 kcal. /gm. and 8 kcal./gm. For present purposes the median value, 7 kcal./gm., has been accepted. In estimating the catabolized energy for a given period, the metabolizable energy is increased or decreased by the caloric equivalent of the change in body weight for the same period.

The ratio of metabolizable energy to catabolized energy, that is, of input to output, provides a measurement of energy balance and will be called the balance coefficient. A value of 1.00 prevails when energy intake is equal to energy expenditure; values above 1.00 result from a positive energy balance with gain in body weight, and conversely. This coefficient should not be confused with the *Energiebilanz* of Rautenberg (1957), which denotes a different ratio.

In 1955, the metabolizable energy was measured continuously by successive 7-day periods. In 1956, it was considered desirable to follow variation in energy metabolism in greater detail and the period was reduced to 4 days. The birds were weighed at the beginning and end of each metabolism period and the state of molt was recorded. Weighings were uniformly made between 11:30 a.m. and 12:30 p.m. This routine time was selected as preferable to the pre-dawn weighings which many European investigators employ (see, for example, Rautenberg, 1957; Merkel, 1958). If variation in body weight is to be utilized as an index of premigratory fattening, as in these investigations, it seems inadvisable to weigh the birds at dawn, immediately following a night of *Zugunruhe* (see beyond) during which 15 to 20 per cent of the body weight may be dissipated to supply energy for muscular activity.

Measurement of standard metabolic rate.—The respiratory metabolism of birds in standard physiological conditions (28°C. ambient temperature, quiescent at night, after 3 to 4 hours of fasting; see King and Farner, 1961) was determined in a small modification of the volumetric device developed by Schwabe and Griffeth (1938), who describe in detail its structure and operation. The maximum error in the estimation of oxygen consumption and carbon dioxide production was about three per cent. The coefficient of variation in 25 calibrations was 2.05, which included the error in the measurement of the graphic record. All gas volumes were reduced to standard conditions (760 mm. Hg, 0°C., dry). The standard metabolic rate determined in this manner approximates the minimum or "basal" energy expenditure of the birds in a thermoneutral environment.

Measurement of activity.—Concurrently with the measurements of energy intake and expenditure, the activity (movement) of each bird in its metabolism cage was continuously sampled. This was accomplished by a modification of the apparatus described by Farner and Mewaldt (1953). Movements of a central perch-microswitch assembly

in each cage were detected separately by an Esterline-Angus operations recorder and an impulse counter. A numerical total of perch movements was recorded for each hour of the day. A continuous graphic and numerical index of movement within each cage was thus available. These data clearly do not yield an absolute measurement of activity, but they do give an activity index as a fraction of total activity. For individual birds this is a relatively constant fraction. Shortly after confinement to small cages the birds de-

TABLE 1

MEAN DATA ON ENERGY METABOLISM OF SIX MALE *Zonotrichia leucophrys gambelii* EXPOSED TO NATURAL TEMPERATURE AND PHOTOPERIOD

Interval	Body weight in grams		Metabolizable energy Kcal./bird/day		Catabolized energy Kcal./bird/day		Ambient temperature
	Mean	SD	Mean	SD	Mean	SD	Mean °C.
1955							
Mar. 8–20	26.3	1.4	25.73	1.11	25.5	1.8	—0.3
Mar. 21–31	26.4	1.3	25.52	2.40	25.1	1.9	—0.1
Apr. 1–10	26.2	0.4	24.22	3.27	24.4	4.4	5.7
Apr. 11–20	26.8	2.3	28.15	2.58	25.8	2.5	3.5
Apr. 21–30	32.4	2.9	30.79	2.66	27.3	3.2	4.9
May 1–10	33.3	1.4	22.45	1.19	24.1	1.6	8.6
May 11–20	31.6	2.0	22.53	1.24	24.0	2.2	9.4
May 21–30	30.9	1.4	.....	.....	.....	.....	.....
June 1–10	28.0	2.3	20.48	5.50	22.6	2.2	12.0
1956							
Mar. 16–20	26.8	0.9	.....	.....	.....	.....	.....
Mar. 21–25	26.7	1.0	23.69	1.11	23.4	1.2	8.9
Mar. 26–31	26.8	0.7	23.48	1.56	23.8	2.0	5.0
Apr. 1–5	27.1	3.3	23.21	0.82	23.3	1.2	4.7
Apr. 6–10	26.6	0.9	24.54	1.00	23.4	1.3	7.6
Apr. 11–15	28.3	1.9	26.36	2.80	22.5	1.3	12.1
Apr. 16–20	31.3	2.1	28.23	2.08	24.0	1.6	11.1
Apr. 21–25	33.6	1.2	25.17	2.16	23.1	1.8	12.6
Apr. 26–30	34.5	0.7	23.21	1.71	23.0	0.9	14.7
May 1–5	34.0	0.9	22.26	1.02	23.8	1.3	9.9
May 6–10	33.4	1.1	.....	.....	.....	.....	.....
May 14–20	32.6	0.8	21.19	0.61	21.8	0.9	10.2

velop characteristic and almost invariable exercise patterns which include activation of the recording perch. It is true, however, that different birds exhibit different patterns of movement, and hence that different fractions of the total activity are recorded. For this reason, the data must be interpreted and compared on a relative basis as an activity pattern. This problem is discussed at length by Farner, Mewaldt, and King (1954).

In the present investigation the activity data were used chiefly to detect the onset and development of nocturnal migratory restlessness, or *Zugunruhe*. There no longer appears to be any significant doubt that this phenomenon (see reviews by Eyster, 1954; Farner, 1955; Weise, 1956; Lack, 1960) is the expression by caged birds of the urge to migrate. It is therefore an adequate index of the time at which migratory behavior is "released." The similarity between the onset of *Zugunruhe* in captive birds and the timing of northward migration in the wild populations has already been demonstrated in several forms of *Zonotrichia* (Farner, King, and Wilson, 1957). The most conspicuous change in the diurnal activity pattern as *Zugunruhe* develops in spring is a burst of activity which begins at twilight and continues at a high level through midnight (Farner, Mewaldt, and King, *op. cit.*). Accordingly, the activity during this period has

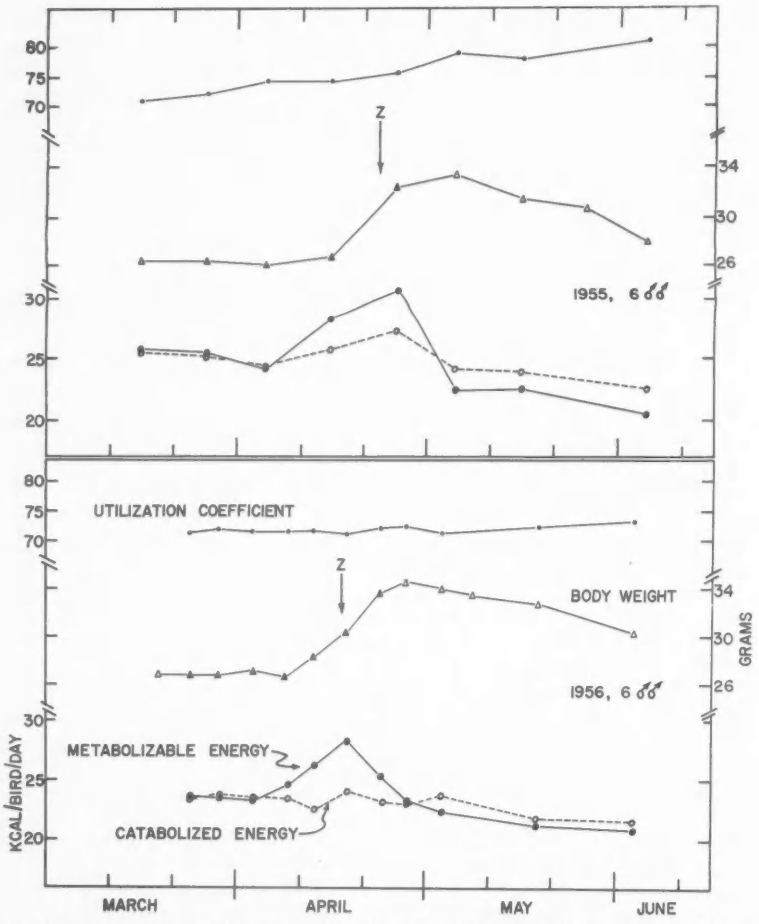

Fig. 1. Averaged data for White-crowned Sparrows confined out of doors. The curves and units labeled in the lower panel have the same significance in the upper panel. The Z-arrow indicates the beginning of *Zugunruhe*. The intensity of molt is shown by the triangles of the body weight curve as heavy molt (solid), medium or light molt (half-filled), or no molt (open).

been taken as a *Zugunruhe* index, expressed as the mean "recorded hops per hour" for the 4-hour period between 8 p.m. and midnight.

RESULTS

The averaged data for all six birds are compiled in tables 1, 2, 3 and in figures 1, 2, and 3. In these summaries, the data for 1955 and 1956, except for the standard metabolic rates, have been averaged by 10-day and 5-day intervals, respectively. In this proce-

dure, those "median dates" (in 1955 the initial date of the metabolism period plus 3 days; in 1956, initial date plus 2 days) which fell within the interval indicated were included in the average value for that interval. This statistical procedure leads to a slight reduction of maximum average values because the attainment of maxima was not precisely coincident in all of the birds. However, the pattern of variation was so similar quantitatively and qualitatively in all the individuals in the two years that it is not justifiable to use the space necessary to display complete data for each individual. The averaged data represent faithfully the changes characteristic of the premigratory period.

TABLE 2

MEAN BALANCE COEFFICIENT AND UTILIZATION COEFFICIENT IN SIX MALE *Zonotrichia leucophrys gambelii* EXPOSED TO NATURAL TEMPERATURE AND PHOTOPERIOD

Interval	Balance coefficient Mean	Utilization coefficient Mean	SD
1955			
Mar. 8–20	1.01	70.7	2.1
Mar. 21–31	1.02	72.1	2.2
Apr. 1–10	0.99	74.5	2.1
Apr. 11–20	1.09	74.4	1.7
Apr. 21–30	1.13	75.9	2.2
May 1–10	0.93	78.9	2.2
May 11–20	0.94	78.0	3.2
May 21–30	.....	.....	....
June 1–10	0.91	80.8	1.6
1956			
Mar. 21–25	1.01	71.2	1.0
Mar. 26–31	0.99	71.7	1.4
Apr. 1–5	1.00	71.5	1.9
Apr. 6–10	1.05	71.4	1.4
Apr. 11–15	1.17	71.6	1.9
Apr. 16–20	1.18	71.1	1.4
Apr. 21–25	1.09	72.0	2.2
Apr. 26–30	1.01	72.2	2.3
May 1–5	0.94	71.2	2.0
May 6–10	.....	.....	....
May 14–20	0.97	72.3	2.1

Body weight.—All six of the birds in 1955 and 1956 exhibited typical premigratory fat deposition. There was a precipitant increase in body weight which began in mid-April and reached a peak about the first of May. In 1955, the median date for the onset of fat deposit was April 17 ± 4 days; in 1956, it was April 13 ± 3 days. The percentage weight increase, as computed from the mean values in table 1, was 27 in 1955 and 30 in 1956.

After reaching its peak in early May, the body weight began immediately to decline toward a midsummer low which was reached in June and early July at about the time of the start of postnuptial molt. The period of maximum and declining body reserves thus corresponds approximately with the spring migration and early breeding season of the wild population.

Energy intake and utilization.—The principle change in the energy economy associated with the development of the premigratory fat reserves was a sudden increase in metabolizable energy income. This resulted almost entirely from a large increase in gross energy intake, that is, from an increase in appetite. The median date at which increase in gross energy intake became apparent in 1955 was April 9 ± 2 days; in 1956

the initial date was also April 9 ± 3 days. The daily energy expenditure (catabolized energy) of the birds in general increased during the active phase of fat deposition, although in one individual in each year an initial decline in this energy fraction contributed part of the surplus energy deposited as fat. The mean balance coefficients are summarized in table 2. The development of premigratory fat deposits in different individuals is associated with a maximum energy income some 16 to 35 per cent in excess of energy expenditure. The mean maxima shown in table 2 are somewhat lower because of slight temporal differences in attaining peak values.

The variation in the utilization coefficient was small but showed some definite differences in the two years of the investigation. In 1955, it increased from an initial value of about 71 to a level of about 81 in early June, with a maximum rate of increase coinciding roughly with the period of maximum gain in weight. In 1956, there was no important increase in the utilization coefficient.

The standard metabolic rates were determined only in 1956, with results shown in table 3. The averages in each case represent the data from the group of six birds as studied individually over a period of 6 to 8 days. Because of the desirability of making the metabolism determinations at strictly comparable times of the night (11:30 p.m. to 12:30 a.m.), it was possible to make only one determination per night. The date which accompanies each average in table 3 is the median date for the period. It appears from these data that the absolute metabolic rate, expressed on a "per bird" basis was essentially unaltered during the premigratory period. Because of the large dispersion of the individual values there are no statistically significant differences among the means. The 13 per cent increase in the means between April 10 and April 21 thus may or may not be a physiological reality. It is worthy of note, however, that it corresponds in part with the prenuptial molt, which has often been associated with an increase in metabolic rate (Schildmacher, 1952; Wallgren, 1954).

TABLE 3

STANDARD METABOLIC RATE AT 28°C. OF SIX MALE *Zonotrichia leucophrys gambelii* DURING THE VERNAL PREMIGRATORY PERIOD, 1956

Date	Ml. O_2/bird/hr. Mean	SD	Mean R. Q.	Kcal./bird/day Mean	Body weight Mean
March 24	126.7	20.2	0.79	14.56	26.0 gm.
April 2	129.2	23.2	0.78	14.82	25.6
April 10	120.3	27.5	0.79	13.83	26.0
April 21	136.1	16.9	0.80	15.68	30.7
April 30	132.4	20.7	0.79	15.22	32.9
May 10	130.0	17.5	0.78	14.91	33.8

It should be noted also that the standard metabolic rate of these birds is considerably higher than the minimum standard rate for birds of similar size. The minimum mean rate in 4 weight-matched male *Z. l. gambelii* in November and December was about 8.6 kcal./bird/day (King and Farner, 1961). The higher rate in the present investigations was undoubtedly due to the decreased depth of sleep (Bergman, 1950) and overt nocturnal restlessness associated with the approach and development of *Zugunruhe*. Merkel (1958) discusses this problem in relation to other species. It is not possible to establish, short of anesthetizing the birds, just how much of such an increase is a result of real alteration of maintenance metabolism, if any, and how much is due simply to wakefulness and increased muscular tonus.

Prenuptial molt.—No quantitative measurements of the intensity of molt were undertaken. Molt was arbitrarily classed as light, medium, or heavy. In general, birds in light molt had about a dozen feathers in sheaths in the spinal, ventral, or capital tracts. Birds in heavy molt had the pinfeathered appearance characteristic of intensive plumage growth. Although this method of classification is clearly subjective, it provides satisfactory comparative data when applied consistently by a single investigator.

It is evident from inspection of the molt symbols on the weight curves in figure 1

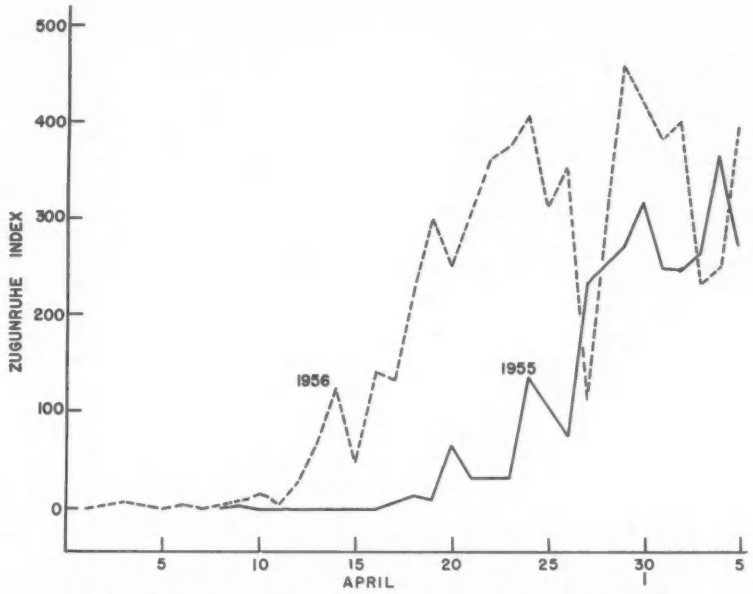

Fig. 2. Average *Zugunruhe* index for six male White-crowned Sparrows.

that the intensity of molt was declining at the onset of vernal fat deposition. By the time the maximum weight was attained, most of the birds had finished the prenuptial molt or were showing only very light molt. This appears to agree very well with the sequence observed in wild populations (King and Farner, 1959).

Zugunruhe.—The development of migratory restlessness is shown as the *Zugunruhe* index in figure 2. Although the onset of *Zugunruhe* in several of the birds was quite abrupt, especially in 1955, when environmental temperature was lower, the change in the activity pattern of other individuals was comparatively gradual. In these cases it is difficult to state a definite date for the beginning of *Zugunruhe*. Hence, in order to establish comparative data, *Zugunruhe* is considered to begin in these individuals on the date when the *Zugunruhe* index exceeded a mean value of 100 hops per hour.

It is evident from figure 2 that nocturnal activity began to develop on about April 17 in 1955 and was well established by April 24. The median date for the start of *Zugunruhe*, as determined from the data for individual birds, was April 24 ± 4 days. In 1956, nocturnal activity began to diverge from premigratory levels on April 12 and more or

less steadily increased after April 15. The median arbitrary date for the onset of *Zugunruhe* was April 17 ± 4 days. In general, it appears that the development of *Zugunruhe* coincides with an increasing or maximal positive energy balance and with the active phase of vernal fattening. It is clear, however, that the maintenance of *Zugunruhe* is not dependent upon the continuation of a positive energy balance *per se*. The duration of *Zugunruhe* is correlated better with the period of excess reserves of fat. The records for the summer months show that nocturnal activity declines and ceases as the body weight diminishes to its base level in the first half of July.

Ambient temperature.—The mean ambient temperature of the outdoor laboratory is summarized in table 1 for each of the metabolism periods. The mean values were obtained by averaging the daily minimum and maximum temperatures for the period. It can be seen that the premigratory period in 1956 was considerably warmer than in the preceding year. This has caused a general downward displacement of the metabolizable energy curve as a consequence of decreased thermoregulatory expenditure. During the periods associated with the start of fat deposition, the mean temperature was considerably different in the two years of the investigation. In 1955, comparing the periods of April 1 to 10 and April 11 to 20, it is evident that fat deposition started after a large increase in temperature (from −0.1°C. to 5.7°C. during April 1 to 10), but it was concurrent with a period of moderate temperature decline. In 1956, fat deposition was preceded and accompanied by a period of rapidly increasing temperature. It should be noted that the mean catabolized energy, which includes the thermoregulatory expenditure, was relatively stable during these periods.

DISCUSSION

Several hypotheses concerning the energy sources for migratory fat deposition require examination in relation to the present data for the White-crowned Sparrow. It has been recognized generally that a positive energy balance is a prerequisite for any accumulation of fat. Obviously, input must exceed output. The hypotheses which have been advanced to explain all or part of this positive balance appear to fall into one or the other of the following classes: (1) The positive balance results from a premigratory alteration in the partitioning of a more or less constant energy income, that is, a decline in maintenance fractions with a consequent increase in "surplus" energy which may be stored as fat. This may be called the "energy-sparing" hypothesis. (2) The positive balance results from an adaptively increased energy income which periodically exceeds energy output as the birds establish and replenish their fat reserves. There is no reason to regard these concepts as mutually exclusive, although it seems that they previously have been regarded as alternative points of view.

With regard to the first type, Groebbels (1928, 1930, 1932) originated the idea that a premigratory decline in standard ("basal") metabolism spares energy which can be used in fat deposition. However, there is no acceptable experimental evidence that the maintenance metabolism declines during the premigratory period. In the present investigation, the standard metabolic rate was essentially constant during March and April. It is clear also from the data on catabolized energy that there was no amelioration in energy expenditure which could spare calories for fat deposition. In addition, there are good data from other migratory passerines which show that the standard metabolism is not significantly diminished during the premigratory periods (Koch and de Bont, 1952; Wallgren, 1954; Rautenberg, 1957 [cf. King, 1958]; Merkel, 1958).

Another energy-sparing hypothesis is that of Wachs (1926), who proposed that the efficiency of energy utilization increases during the migratory periods. Any such increase,

as measured by the utilization coefficient in the present investigation, will reduce the relative energy cost of food procurement, but the efficiency factor becomes limiting, as is the case with any energy-sparing mechanism, only when some relative limit is placed upon energy intake or the stimulus for energy intake. This may occur during periods of food scarcity or under extreme metabolic stress when the organism has attained the maximum rate of absorption from the gut. The White-crowned Sparrow, even at the northern boundary of its winter range, only rarely encounters the first situation and probably never faces the latter (see Kendeigh, 1949; Seibert, 1949; and West, MS, for data on the limits of energy absorption in small birds). However, in the interests of exploration, the potential contribution of increased efficiency of utilization with constant gross energy intake (28.6 kcal./bird/day) and constant catabolized energy output (20.0 kcal./bird/day) has been assessed. It is assumed that the utilization coefficient increased by 0.33 units/day (equal to the maximum rate of increase in 1955). In this sample, an energy surplus equivalent to about 3.2 gms. of adipose tissue will accumulate during a period of 24 days. The body weight thus hypothetically increases by about 0.13 gms./day. The change in the efficiency function may potentially contribute a small but appreciable fraction of the vernal weight increment and may have done so in the birds studied in 1955. In 1956, however, the utilization coefficient was essentially constant during the premigratory period, indicating that increase in efficiency is not a necessary concomitant of vernal fattening in the White-crowned Sparrow. Other migratory species have not as yet been studied in this regard.

The most prominent of the energy-sparing hypotheses is that first suggested in rudimentary form by Groebbels (1932), fully developed by Kendeigh (1934, 1949), and advocated by several subsequent investigators (Seibert, 1949; Davis, 1955; West, 1960). According to this viewpoint, the surplus energy for storage as fat originates at least in part with (a) the energy-sparing effect of declining thermoregulatory demands as the ambient temperature increases in spring, (b) the energy-sparing effect of the cessation of molt, if any, and (c) the increasing time available for feeding as the daily photoperiod increases in spring. This hypothesis necessarily assumes that there is a significant inertia or "physiological lag" (Davis, 1955) in the regulatory systems which correlate energy intake and energy expenditure. As the intensity of energy-demanding functions declines in spring, it is supposed that energy intake continues temporarily at its former high level because of inertia in the regulatory system.

We submit that the present data for the White-crowned Sparrow cannot be rationalized on the basis of energy-sparing mechanisms or a repartitioning of the energy expenditure during the premigratory period. The major source of energy deposited in fat derives from a marked increase in energy income with constant or slightly elevated energy expenditure (catabolized energy) during the premigratory period. The birds have exhibited a definite hyperphagia (King and Farner, 1956), or increase in appetite, and there has to be an upward shift in the regulated level of body reserves. This is in agreement with data from investigations of the White-throated Sparrow, *Zonotrichia albicollis* (Odum and Major, 1956; Weise, 1956), Slate-colored Junco, *Junco hyemalis*, and Tree Sparrow, *Spizella arborea* (Weise, 1956), Chaffinch, *Fringilla coelebs* (Koch and de Bont, 1952), and the Whitethroat, *Sylvia communis*, and European Robin, *Erithacus rubecula* (Merkel, 1958).

With regard to the importance of increased feeding time with increasing daily photoperiod in spring, it would appear from data presented in figure 3 that this has no marked significance. Energy intake per hour declines in a regular manner, except for the superimposed period of over-eating, and shows no evidence of "physiological lag." Exclusive

of the period of increased intake, the rate of energy intake declines seasonally faster than the photoperiod increases. It is difficult to see how the slow, regular increments in daily photoperiod have any permissive relation to this increase in appetite. It is equally difficult to rationalize the increase in the hourly rate of energy intake on the basis of a "physiological lag" mechanism. Support for this viewpoint comes also from the investiga-

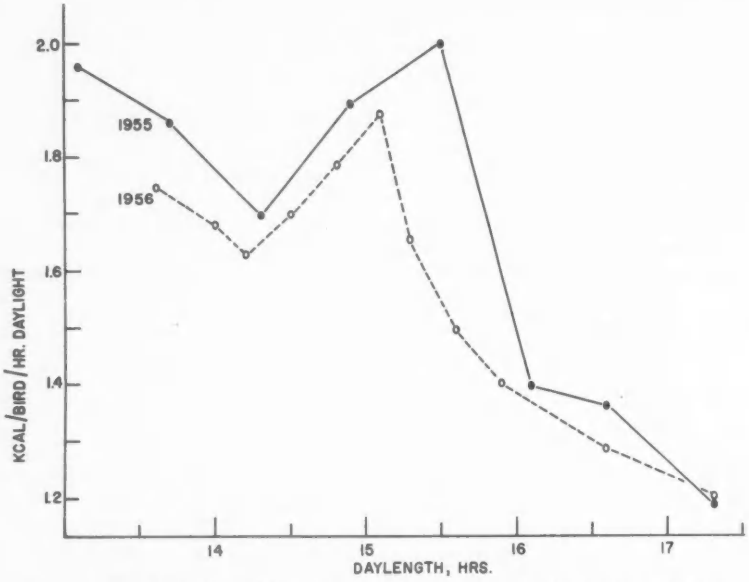

Fig. 3. Average metabolizable energy as a function of daylength (including civil twilight) from March to June in six male White-crowned Sparrows.

tions by Koch and de Bont (1952) of migratory and sedentary races of *Fringilla coelebs* subjected at 10°C. to a photoperiod which was gradually increased from 8 to 16 hours per day. Food consumption by the member of the sedentary race fluctuated around a gradually increasing mean as the duration of the photoperiod increased. This bird did not become fat. In the member of the migratory race there was a definite increase in energy intake which lasted for about 7 days and a corresponding increase in body weight from about 20 gms. to about 28 gms. Although the evidence would be more gratifying if more than one individual of each race had been studied, the data nonetheless show that increased time for feeding is not alone sufficient to induce fat deposition. There must also be the hereditary capacity, which evidently exists in certain migratory species but not in the sedentary ones, for the metabolic response to light stimulation.

It thus appears from the data assembled here that the major source of energy for the establishment of premigratory fat reserves in several species of passerines does not derive from passive sparing mechanisms, but from a strong stimulation of appetite which leads to simple over-eating. The role of energy-sparing mechanisms in other species, particularly those which overwinter in marginal environments, may of course assume

greater importance than is evident in the White-crowned Sparrow. It is widely agreed that migratory fat deposition is an important adaptation in small birds, but different species very possibly emphasize different sources of energy.

Adaptive hyperphagia cannot be demonstrated in the wild population by direct methods. However, we have previously emphasized the striking similarity between wild and captive birds in the events of the premigratory period, including the timing and rate of fat deposition (King and Farner, 1959). There does not appear to be any reason to believe that the metabolic changes which accompany this fat deposition are basically different in wild and captive populations. As a working hypothesis, we therefore assume that adaptive increase in appetite occurs also in the wild population from which we have obtained our experimental birds.

Consideration of the differences in nocturnal work by wild and captive birds, however, leads to the conclusion that the pattern of hyperphagia must be somewhat different in the wild birds and that it must persist throughout the migratory season. The energy expenditure and weight loss of a night of migratory flight must be considerably greater than during a night of *Zugunruhe* in a small cage. In the captives, hyperphagia is detected only during the initial deposition of fat in the premigratory period. After this new level of reserves is established it can of course be maintained without increased intake if the total energy expenditure does not increase. The data on catabolized energy indicate that the total daily energy expenditure is not greatly changed in the caged birds during the period of *Zugunruhe*, and they imply that there is merely a shift between daytime and nighttime expenditure. This situation is very similar to the energetics of "active" and "static" obesity in laboratory mammals (Mayer, 1955).

It should perhaps be emphasized that the negative balance coefficients observed during May and June reflect only the long-term regulation of body reserves around a slowly decreasing mean. Because the metabolism determinations occupied 4- to 7-day periods in the present investigation, the balance coefficient does not provide information about the short-term, day-to-day regulation of energy intake. For this reason we have not directly demonstrated the persistence of hyperphagia in these investigations.

In view of this deficiency, a pilot experiment was undertaken during the period of autumn *Zugunruhe* in 1956. Three male *Z. l. gambelii* which had established migratory fat reserves and which were exhibiting nocturnal activity were periodically starved to a nonmigratory level of body weight (24–25 gms.). It was reasoned that in the absence of some special stimulus to appetite the fat reserves would not be restored. The results of this experiment are shown in figure 4. It is evident that the body reserves were rapidly restored to what appeared to be an increasing maximum as the season progressed, indicating that there was an active regulation of the magnitude of body reserves. The rapidity with which these reserves were restored following depletion can be explained only by the same mechanism of hyperphagia through which they were originally established. This experimental procedure provides a method for detecting the existence of potential hyperphagia and for identifying the regulated level of body reserves. It is desirable that it be applied to the vernal migratory period, together with measurements of energy intake, in order to confirm the inferences made previously.

The pattern of weight variation shown in figure 4 probably conforms qualitatively with what happens in wild birds during migration. Zimmerman (quoted by Wolfson, 1954) stated that *Zonotrichia albicollis* appears to move northward in jumps of at least 300 miles at intervals of 7 to 10 days. Analysis of trapping and retrapping data for this species, however, indicates that the stop-over time is somewhat less, averaging 3 to 5 days (Stack and Harned, 1944; Borror, 1948; Blake, 1950). It may be assumed that the

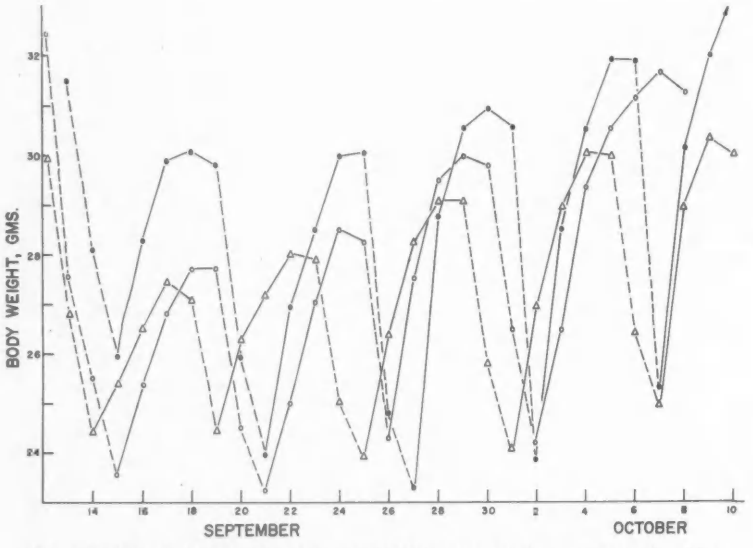

Fig. 4. Variation in body weight of three male White-crowned Sparrows as produced by intermittent fasting (broken line) and re-feeding *ad libitum* (solid line).

birds arrive at the stop-over point in a state of depleted or at least decreased fat reserves. The persistence of adaptive hyperphagia assures that the body reserves will be rapidly restored. Wolfson (1954) has shown that the time required by *Zonotrichia albicollis* to increase its fat deposits from "none" to "heavy" when supplied with ample food is 4 to 6 days, or about the same as the apparent stop-over time. It can be seen from figure 4 that *Z. l. gambelii* can increase its body weight to a maximum in about 3 to 5 days.

SUMMARY AND CONCLUSIONS

Energy intake, energy expenditure, body weight, and nocturnal activity (*Zugunruhe*) were studied in captive males of the White-crowned Sparrow of the race *Zonotrichia leucophrys gambelii* during March to June of two successive years. The birds were exposed out of doors to essentially normal weather conditions and photoperiod.

During the second week of April in both years all of the birds exhibited an abrupt increase in gross energy intake (hyperphagia) and a simultaneous deposition of migratory fat. Total energy expenditure in most birds was practically unchanged during this period, indicating that the only significant source of surplus calories was from the increased intake. Nocturnal activity began several days after the beginning of fat deposition and the termination of the prenuptial molt.

It is emphasized that energy intake and the variation in the level of body reserves are regulated functions. During the premigratory and migratory periods it is evident that the characteristics of the regulatory systems are adaptively altered to provide a much increased level of reserves of fat. One of the obvious elements of this adaptation is a strong stimulus to appetite which probably persists throughout the migratory period and assures that fat reserves will be replenished rapidly during stop-over periods in the migratory itinerary.

LITERATURE CITED

Bergman, G.
1950. Experimentella undersökningar över sömndjupet hos olika småfågelsarter. Ornis Fennica, 27:109–124.

Blake, C. H.
1950. Length of stay of migrants. Bird-Banding, 21:151–152.

Blanchard, B. D., and Erickson, M. M.
1949. The cycle in the Gambel sparrow. Univ. Calif. Publ. Zool., 47:255–318.

de Bont, A. F.
1947. Le métabolisme des graisses chez les oiseaux migrateures et sédentaires. Le Gerfaut, 37:57–62.

Borror, D. J.
1948. Analysis of repeat records of banded white-throated sparrows. Ecol. Monog., 18:411–430.

Davis, E. A., Jr.
1955. Seasonal changes in the energy balance of the English sparrow. Auk, 72:385–411.

Eyster, M. B.
1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monog., 24:1–28.

Farner, D. S.
1955. The annual stimulus for migration: experimental and physiologic aspects. *In* Recent Studies in Avian Biology (Univ. Illinois Press, Urbana), pp. 198–237.

Farner, D. S., King, J. R., and Wilson, A. C.
1957. The development of vernal migratory behavior in caged individuals of several taxa of *Zonotrichia*. Anat. Record, 128:546.

Farner, D. S., and Mewaldt, L. R.
1953. The recording of diurnal activity patterns in caged birds. Bird-Banding, 24:55–65.

Farner, D. S., Mewaldt, L. R., and King, J. R.
1954. The diurnal activity patterns of caged migratory white-crowned sparrows in late winter and spring. Jour. Comp. Physiol. Psych., 47:148–153.

Groebbels, F.
1928. Zur Physiologie des Vogelzuges. Verh. Ornith. Gesellsch. Bayern, 18:44–74.
1930. Bausteine zu einer Physiologie und Histophysiologie des Zugvogels. I. Mitteilung: Physiologische Untersuchungen an Helgoländer Zugvögeln. Zeits. vergl. Physiol., 12:682–702.
1932. Der Vogel. Bau, Funktion, Lebenserscheinung, Einpassung. Erster Band: Atmungswelt und Nahrungswelt (Gebrüder Borntraeger, Berlin).

Helms, C. W., and Drury, W. H., Jr.
1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding, 31:1–40.

Kendeigh, S. C.
1934. The role of environment in the life of birds. Ecol. Monog., 4:299–417.
1949. Effect of temperature and season on the energy resources of the English sparrow. Auk, 66:113–127.

Keys, A., and Brozek, J.
1953. Body fat in adult man. Physiol. Rev., 33:245–325.

King, J. R.
1958. Review of "Vergleichende Untersuchungen über den Energiehaushalt des Bergfinken (*Fringilla montifringilla* L.) und des Haussperlings (*Passer domesticus* L.)." W. Rautenberg (Jour. für Ornith., 98:36–64, 1957), Bird-Banding, 29:61–64.

King, J. R., and Farner, D. S.
1956. Bioenergetic basis of light-induced fat deposition in the white-crowned sparrow. Proc. Soc. Exper. Biol. Med., 93:354–359.
1959. Premigratory changes in body weight and fat in wild and captive male white-crowned sparrows. Condor, 61:315–324.

1961. Energy metabolism, thermoregulation, and body temperature. *In* Biology and Comparative Physiology of Birds (Academic Press, New York), pp. 215–288.

Koch, H. J., and de Bont, A. F.

1952. Standard metabolic rate, weight changes and food consumption of *Fringilla c. coelebs* L. during sexual maturation. Ann. Soc. Roy. Zool. Belg., 82:143–154.

Lack, D.

1960. The influence of weather on passerine migration. A review. Auk, 77:171–209.

McGreal, R. D., and Farner, D. S.

1956. Premigratory fat deposition in the Gambel white-crowned sparrow: some morphologic and chemical observations. Northwest Sci., 30:12–23.

Mayer, J.

1955. Regulation of energy intake and body weight: The glucostatic theory and the lipostatic hypothesis. Ann. N. Y. Acad. Sci., 63 (art. 1): 15–43.

Merkel, F. W.

1958. Untersuchungen über tages–und jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. Zeits. vergl. Physiol., 41:154–178.

Odum, E. P., and Major, J. C.

1956. The effect of diet on photoperiod-induced lipid deposition in the white-throated sparrow. Condor, 58:222–228.

Rautenberg, W.

1957. Vergleichende Untersuchungen über den Energiehaushalt des Bergfinken (*Fringilla montifringilla* L.) und des Haussperlings (*Passer domesticus* L.). Jour. für Ornith., 98:36–64.

Schildmacher, H.

1952. Stoffwechselphysiologische Studien an männlichen Gartenrotschwänzen *Phoenicurus ph. phoenicurus* (L.). Biol. Zentralblatt, 71:238–251.

Schwabe, E. L., and Griffeth, F. R., Jr.

1938. An easily constructed rat metabolism apparatus which automatically records oxygen consumption and animal activity. Jour. Nutrition, 15:187–198.

Seibert, H. C.

1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk, 66:128–153.

Stack, J. W., and Harned, R. L.

1944. Seventeen years of banding white-throated sparrows and slate-colored juncos at Michigan State College. Bird-Banding, 15:1–14.

Wachs, H.

1926. Die Wanderungen der Vögel. Ergeb. Biol., 1:479–637.

Wallgren, H.

1954. Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. Acta Zool. Fennica, 84:1–110.

Weise, C. M.

1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, 37:275–287.

West, G. C.

1960. Seasonal variation in the energy balance of the tree sparrow in relation to migration. Auk, 77:306–329.

Wishnofsky, M.

1958. Caloric equivalent of gained or lost weight. Amer. Jour. Clinical Nutrition, 6:542–546.

Wolfson, A.

1942. Regulation of spring migration in juncos. Condor, 44:237–263.

1954. Weight and fat deposition in relation to spring migration in transient white-throated sparrows, Auk, 71:413–434.

Department of Zoology, Washington State University, Pullman, Washington, July 29, 1960.

MOLT CYCLES IN EQUATORIAL ANDEAN SPARROWS

By Alden H. Miller

A principal finding in a year-long study of an equatorial population of Andean Sparrows (*Zonotrichia capensis*) in Colombia was that each individual displays two breeding periods in one year (Miller, 1959). This is particularly clear in males in which there are two complete regressions and two full regrowths of the testis over a 12-month period, the 6-month norm for the completed cycle reflecting an innate cyclic tendency which is only partly coerced by the rainfall cycle. At least some individuals in full reproductive capacity and some actual nestings may be found in every month of the year.

In north temperate and arctic passerine birds it has long been recognized that among the non-migratory species the single, complete, annual molt follows the nesting period, and it has often been thought that this molt was physiologically related to the reproductive cycle, being an expression in part of the drastic changes in hormonal balance that inevitably occur in the regressive period of the hypothalamic-pituitary-gonad mechanism. Experimental results in recent years, particularly in respect to the prenuptial molt, have tended to show a partial independence of the physiologic control of molt and the gonadal cycle (see, for example, Miller, 1954:18, and Selander, 1958:366). But in any event from the ecologic and adaptive standpoint it has become increasingly clear that molt and nesting are functions which compete for energy and food resources and that the two, by whatever stimulating and physiologic mechanisms, are neatly timed in various ways to avoid a simultaneous drain on the bird and its environment. These matters have been especially brought to notice and analyzed by Pitelka (1958).

In the light of these several circumstances it was surprising to find in equatorial populations of *Zonotrichia capensis* that two complete "annual" molts occur each year and that there are no partial, prenuptial molts. Moreover both a linking and a degree of independence of the schedules of molts and breeding states were observed and these matters require detailed exploration for their various implications. The complete molt in equatorial passerines is no less taxing a process than in northern species, if, as often proves true, it is pursued almost as rapidly as in northern types. Pitelka (1958) has shown that in the Steller Jay (*Cyanocitta stelleri*) the dry weight of the plumage mass represents about 10 per cent of the total weight of the bird and the assumption of a similar relation in Andean Sparrows suggests the appreciable energy drain in producing the plumage over a two-month period in addition to other normal activities.

METHODS

The general setting for this work and the procedure in following the cycles of individuals has been described in part in earlier papers (1958; 1959). Throughout I was aided in trapping birds and recording weather by Virginia D. Miller and our daughters, Barbara and Patricia. Acknowledgment also is gratefully made of support by a Guggenheim fellowship and of aid by F. Carlos Lehmann V. of the Universidad del Valle, Colombia.

The particular data on molt were derived in three ways. (1) The 160 banded individuals trapped and marked in an area of about 4 acres, from February 10, 1958, to January 22, 1959, were retrapped as often as possible, and on almost all occasions they were examined for molt. Thus in the year a total of 720 capture and recapture records was made; multiple captures on a single day are not included. (2) Color-marked birds identified as individuals and closely followed with binoculars at close range were recorded as in molt when they showed conspicuous breaks in plumage of the body, wing, and tail.

(3) A total of 78 individuals was collected off the study area but within 2 miles of it in similar pasture areas and second-growth bush lots. These were preserved as skins or skeletons and the gonads and some other organs saved for histologic sections. Molt stages were recorded for each.

A series of molt stages has been devised (table 1) to which our raw data on condition of feather replacement can be related. Concordance of molt activity in different feather tracts is broadly similar to that in other northern passerines (see, for example, Miller, 1928:411, table 5, and Pitelka, 1945:245, table 4), but there is greater variability (see p. 147) such that one cannot combine data effectively from different tracts in recording stages as Pitelka (1958:39–41) did for Steller Jays. The most meaningful, protracted replacement process is that of the primaries and this will be used as a basis for registering stages of molt. The orderly sequence of replacement from primary no. 1 to no. 9 is seldom violated, and then only in a minor way, and the replacement of these feathers almost spans the entire molt process.

TABLE 1

STAGES OF COMPLETE, ADULT MOLT

1. Body feather replacement started or replacement in progress in tracts other than primaries (this stage may be omitted and the molt begin with stage 2).
2. Primary 1 (innermost) dropped or regrowing; nos. 2–9 old.
3. Nos. 3–9 old.
4. Nos. 4–9 old.
5. Nos. 5–9 old (inner secondary molt, nos. 7, 8, 9, usually begins).
6. Nos. 6–9 old (outer secondary molt, nos. 1 and 2, usually starts).
7. Nos. 7–9 old.
8. Nos. 8–9 old.
9. No. 9 old.
10. Nos. 8 and 9 new, short; several secondaries still molting.
11. A few secondaries still not full length and/or late traces of body molt and sheath remnants present on outer primaries.

In addition, in the appraisal of the history of an individual, stage of wear, especially of the remiges, was made in order to judge whether a complete molt had or had not occurred recently. It is to be recalled that since there is no perfect coordination of gonad or molt cycles in all individuals of a population, no assumptions about recent molt history can be made on the basis of date alone.

As explained elsewhere (Miller, 1958) age of many of the birds captured was determined by a simple skull operation and reproductive state was ascertained by external evidence in the form of brood patches and the development of the male cloacal gland and by laparotomies. These approaches often enabled us, using also observational records at nests, to relate quite closely age and reproductive and molt histories of individuals.

SEQUENCE OF MOLTS AND PLUMAGES

The sequence of molts and plumages is simple in this species. The natal down is largely lost just after the fledgling period when it wears off the tips of the juvenal feathers to which it adheres, as is usual in passeriform birds. The juvenal plumage is followed by a postjuvenal molt which is incomplete, most notably failing to involve the remiges. The next molt is the complete or adult type of molt engaged in thereafter at approximately six-month intervals. There are no special, partial prenuptial molts. Moreover, once the juvenal body plumage is fully replaced in the postjuvenal molt, the appearance

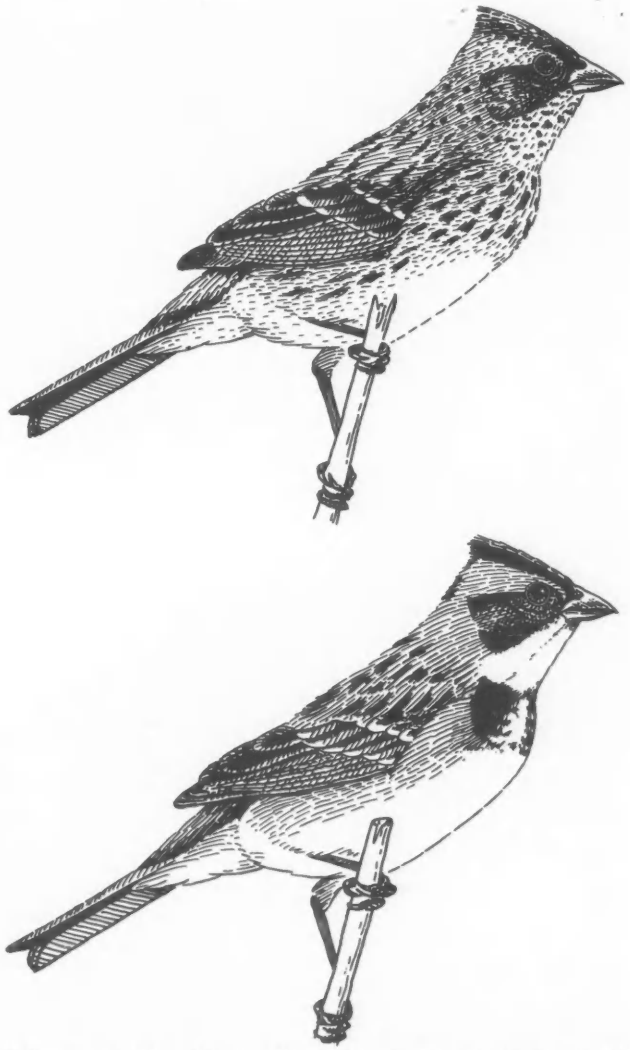

Fig. 1. Plumages of Andean Sparrows (*Zonotrichia capensis*), three-fourths natural size. Drawings by Gene M. Christman based on live birds and showing crest elevated in normal alert attitude. Areas posterolateral to black spot at base of neck are rufous in adult.

of the bird is stabilized in pattern and color at the adult level. An adult-appearing bird, still showing immaturity in the skull, may then at approximately 6 to 8 months of age molt fully from an adult-type plumage to an identical plumage, whether or not it has reached breeding level or engaged in breeding in the preceding interval.

TIME REQUIRED FOR ADULT MOLT

Case histories in some instances are complete enough to show the span of time required for the entire adult molt. There are five records of such molts (table 2) which either run from stage 1 to 10 or 11, or at one or both ends of the process involve records of known lack of molt. These full records indicate minimum spans of 2 months, plus or minus a few days; the case which lacks stage 11 is shorter, at 1 month and 10 days, a history that might well represent a molt completed in 10 days less than 2 months. It is to be noted that this same individual required 2 months for another complete molt six months earlier.

TABLE 2

HISTORIES OF INDIVIDUAL ADULT MOLTS

No. of individual	Stages recorded	Elapsed time*
472 (molt 1)	none–5–6–10–11–none	2 mos., 1 day
472 (molt 2)	none–2–3–10	1 mo., 10 days
466 (molt 1)	none–3–5–none	2 mos., 4 days
482	1–11	2 mos., 2 days
460 (molt 1)	none–M–M–M–M–M–11	1 mo., 29 days
460 (molt 2)	3–9	1 mo., 8 days
466 (molt 2)	3–M–M–10	1 mo., 26 days
840	4–none	1 mo., 17 days
806	none–6–9	1 mo., 27 days
496	4–10	1 mo., 20 days
495	4–6–11	2 mos., 11 days
494	1–3–9	1 mo., 23 days

* Months are all calculated as 30 days.
M = obvious molt seen in field at close range.

Seven other less extended records (table 2), which nonetheless span about four-fifths of the molt stages, are consonant with the foregoing. These show durations of 1 month and 8 days to 2 months and 11 days. Obviously the latter is a case in which the complete molt would extend over at least 2 months and 20 days.

The conclusion to be drawn is then that the adult molt in free-living individuals normally requires 2 months and that the variation, which is rather less than was expected, is represented in probable extremes of 1 month and 20 days and 2 months and 20 days.

The ten stages of the molt, or the eleven stages when number 1 is counted, should require about 6 days each. We have closely examined the record of intervals between stages that are two or three units apart. In calculating the time involved for these short spans, one encounters the danger that the observations could have fallen for any one stage close to the beginning or end of that stage, thus augmenting the apparent variability. Thus if in fact the period from the start of stage 1 to the start of 3 consists of 12 days, at 6 days per stage, the record of successive captures in stages 1 and 3 could be as little as 7 and as much as 18 days apart. Actual inspection of 10 clear-cut two- or three-unit spans shows average time in each ranging from 5 to 12 days per stage with a general average of 8 days. In view of the chances of error in reflecting the exact interval, this figure is not far out of line with that obtained by division of the total time required for molt by the number of stages.

More significant is an inspection of the records to see if longer intervals prevail in the early or late stages of the molt both for two- and three-unit spans and the longer spans (total number of molt history sequences examined is 24). This reveals that most of the 10- to 12-day intervals per stage relate to stages 6 to 11 and most of those

of 5 to 7 days are for stages 1 to 5. We are quite convinced of the trend here indicated, but there are exceptions such that this matter cannot be rigorously quantified. For example, there is one case in which a bird progressed from 6 to 11 at an average of 2 days a stage. But there are no instances of long intervals such as 9 to 12 days for the first four stages whereas there are three instances involving intervals of 2 to 4 days per stage.

It is safe to assume that normally the first four stages proceed more rapidly than the terminal ones, averaging probably 4 days, and that later stages normally are 7 or 8 days. I suspect that stage 11 as defined is usually 10 days long. It is to be recalled that stage 1 may sometimes be skipped.

It is well to note that the total time of 60 days for the complete molt in *Zonotrichia capensis*, here determined directly from living birds, is surprisingly close to Pitelka's calculation of 60 to 70 days for Steller Jays based on molting birds saved as skins. The latter is of course a larger species, but the sample studied was living at 52° to 54° north latitude. Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*), more closely related as fringillids, at 71° N, require 50 to 55 days for the molt (Pitelka, MS). Yet individual House Finches (*Carpodacus mexicanus*) in southern California are occupied for 120 to 150 days with the annual molt (Michener and Michener, 1940:141), and Hawaiian honeycreepers seem to require 3 or 4 months (Baldwin, 1953:322–330).

CORRELATION OF MOLT IN FEATHER TRACTS

The broad relations between activity in the several feather tracts that is generally characteristic of passerine birds prevails in *Zonotrichia capensis* but there is a greater variability in this respect than is usual (compare Miller, 1928:411, and Michener and Michener, 1940:142). If the standard stages based chiefly on the primary molt are used as a base of reference, norms and extremes in certain of the other tracts may be indicated. I gave no detailed attention to precise sequence in certain of the covert series and estimated body replacement as fractions of completion rather than indicating the exact section of the tracts entailed.

Secondaries.—Molt begins in the group of inner secondaries, numbers 7 to 9, and starts separately, always later, with no. 1 and then proceeds in order to no. 6. Thus in fact two sets of replacements occur in this series, probably quite independently. The inner secondaries start molting at stage 5 or 6 (9 instances) and their regrowth probably spans about three stages. Two exceptional initiations at stages 2 and 3 were recorded. We saw no instances of inner secondaries molting or growing later than stage 9.

The outer secondaries in no instance started dropping before stage 6 and never later than stage 7. In one bird they were all replaced by stage 9, but in most individuals two to four old secondaries remain in stage 9 and 1 to 4 in stage 10. By definition, all have at least dropped, although they are not necessarily fully grown, in stage 11. In half of the twelve examples of stage 11, however, all outer secondaries were fully grown.

Wing coverts.—The greater primary coverts molt sequentially from 1 to 9 in coordination with their respective primaries. We saw no exceptions. The alula was noted molting with the outer three primaries.

Greater and middle upper secondary coverts molt in no fixed sequence that could be detected, but more or less en masse. Probably a span of only three stages is required for completion of their growth. Four of ten birds in stages 1 and 2 had begun molting these tracts. Yet six others had not begun by stage 4. A tally of all cases of molt of these coverts shows them fairly evenly spread from stages 1 to 9, but none later. This spread

then reflects chiefly the variation in initiation of the molt over the period from at least stage 1 to 4 and probably from 1 to 5 or 6.

Rectrices.—The tail molt was divided into three stages only since the sequence of dropping of feathers was very irregular even though it tended to be centrifugal. The tail becomes extremely worn in this species and probably it is often partly or entirely removed by accidents. This explains part but not all of the variation in molt. The progressive stages of tail replacement are: A, some or half of old feathers dropped; B, all or nearly all dropped and many partly regrown; C, all old feathers gone and some new feathers fully grown but others short. The correspondence with general molt stages is plotted in table 3; O=no molt as yet; N=fully grown new tail.

TABLE 3

TAIL MOLT IN RELATION TO GENERAL MOLT STAGE

General stage 1	2	3	4	5	6	7	8	9	10	11
A	A	B	O	A	A	B	B	B	A	C
A	O	O	O	A	A	B	B	B	B	C
O	O	O	O	B	A	B	C	B	C	N
O		O	O	B	A	C	C	C	C	N
O		O	O	O	B		C	C	C	N
O		O	O		B		C	C	C	N
O		O	O		B		C	C	C	N
		O			B			N	N	N
					B			N	N	N
					C			N	N	N
									N	N

Thus it is clear that the tail normally molts in the period from stage 5 to 10 but that it can begin with stage 1 or 2; we did not find a case of completion before stage 9.

Body.—As expected, we found that the body molt starts in the center of the ventral and dorsal tracts at about the level of the wings and tends to spread forward and back and to the inner and outer edges of the tracts. Head and neck molt typically marks the late stages of the entire body molt. The downs of the brood patch of females are regrown soon after the start of body molt.

Body molt is designated as follows: O, not yet started; I, started; II, ¼ through; III, ½ through; IV, ¾ through; V, late remnants; N, complete.

Stage 1 of the general molt by definition consists of those cases in which body molt has at least started but the dropping of primaries has not. This early beginning of body molt is unusual in comparison with other passerines such as House Finches, Loggerhead Shrikes (*Lanius ludovicianus*) and Scrub Jays (*Aphelocoma coerulescens*), in which it starts after two primaries have been lost. However, the delayed beginning of body molt is not rare in *Zonotrichia* as shown in table 4 where at least four cases are shown of delay until after stages 3 or 4. Rarely body molt is complete by stage 9 but normally not until stages 10 or 11. Stage 11, it is to be recalled, is partly marked by late remnants of growth either of the remiges or body feathers or both. The usual span of a body molt is over 7 to 9 stages.

Special abnormalities.—Aside from arrested molt and the special circumstances attending it (see p. 154), there are occasional instances of irregular sequence or procedure in the molts of remiges. Occasional instances were noted of replacement of single outer secondaries out of the normal sequence of 1 to 6, and there were two instances of single primaries (nos. 2 and 4, respectively) molting out of sequence in both wings. Also

TABLE 4

BODY MOLT IN RELATION TO GENERAL MOLT STAGE

General stage	1	2	3	4	5	6	7	8	9	10	11
	I	I	O	O	I	II	III	III	III	III	V
	I	I	O	O	III	II	III	III	III	IV	V
	I	I	I	I	III	III	III	III	IV	IV	V
	I	II	I	I	III	III	III	III	IV	IV	V
	I	II	I	I		III	V	III	IV	IV	V
	I	II	I			III		III	IV	IV	V
	I		I			III		IV	V	V	V
	I		I			III			V	V	V
	I		II			III			V	V	V
	I		II			IV			N	V	V
	I		II							V	V
	I										V
	II										N
											N
											N
											N

occasionally the two wings are one stage apart in dropping primaries. The most surprising and functionally significant abnormality was shown by a female that had five new inner primaries and which had dropped numbers 6 to 9 almost simultaneously. These latter were either lacking, distally, in the wing or were so short as to be hardly functional; the bird could barely fly, for this situation prevailed in both wings. In another instance a male had primaries 6 to 9 all short, but irregularly so and with details different in the two wings. Its flight was not seriously impaired at the time, but it may have been earlier as in the female just described.

Summary.—In review, we may point out that the secondary molt, in its sequence and relation to primary molt, is very similar to that of well studied northern passerines. The variations and abnormality in it are no greater than expected from experience with other species. The tail molt is not much more erratic than in other passerines. However, the initiation of body molt shows distinct departure from the norm for passerines, both in the degree of individual variability and the prevalent, perhaps usual, commencement before the inception of the primary molt. The highly irregular schedule of the secondary covert molt is unusual, yet since it seems to be linked with active body molt, its irregularity is perhaps only another expression of the variation in timing of the latter. The two striking instances of abnormalities of primary molt in which a nearly simultaneous loss of four outer feathers occurred, is a situation I have never encountered while examining hundreds of molting passerines in north-temperate areas.

THE DOUBLE ANNUAL CYCLE OF COMPLETE MOLTS

The evidence proving that two adult molts occur each year is presented in table 5. In 20 adult individuals the records show that two complete molts had occurred. These are birds which were far past their postjuvenal molt and the immature period when their trapping and observational histories began. In two instances the records are lengthy enough to show three successive, complete molts spaced roughly at 6-month intervals. Moreover, in no instance did an adequate record of captures of an adult over a span of eight months fail to show evidence of a complete molt. Thus it seems safe to conclude that the double molt is normal, and in so far as we know it always takes place.

The dates entered in table 5 mark the inception of molt at stage 1. When our first record of a molt was for a later stage, the time of stage 1 was estimated on the basis of

the average of 6 days a stage unless a definite record of lack of molt necessitated placing stage 1 subsequent to that date. In two instances stage 1 was estimated partly from close-range observation of a bird outside the trap in which there obviously was a complete-type molt in progress. The extrapolated dates of stage 1 have an estimated reliability of ± 5 days. In many instances the date must be much more accurate than this. In two or three cases possibly an error of 10 days is involved. Where no precise date is

TABLE 5

HISTORY OF ADULT BIRDS SHOWING TWO COMPLETE MOLTS IN ONE YEAR

Bird no.	Molt 1 Date of stage 1	Molt 2 Date of stage 1	Molt 3 Date* of stage 1	Interval between molts in days
844 ♀	Feb. 19	Aug. 10		172
806 ♂	Mar. 10	Aug. 20		163
498 ♀	Feb. 3	X		.....
495 ♂	Feb. 2	X		.....
494 ♀	Feb. 26	Aug. 6		161
488 ♀	Jan. 22	Aug. 2		190
485 ♀	X	Sept. 15		.....
484 ♂	Feb. 28	Sept. 3		185
483 ♀	Jan. 15	July 1		167
482 ♂	Feb. 20	Aug. 2		163
480 ♂	Feb. 19	July 30	Jan. 19	161, 173
478 ♀	Feb. 18	July 6		138
477 ♀	X	July 20		.....
475 ♂	Jan. 10	X		.....
472 ♂	Feb. 17	July 10		143
471 ♀	Feb. 16	Aug. 3		168
470 ♀	Mar. 12	Aug. 1		142
468 ♂	Jan. 15	July 19	Jan. 4	185, 169
466 ♂	Feb.20	Aug. 13		174
460 ♂	Mar. 7	Aug. 13		159
			Total measured intervals	17
			Average interval	165.4 days

* Dates are in 1959 for this molt; all other molts in 1958.
"X" indicates molt known to occur; see text.

entered, but only an X mark, we have conclusive evidence that a complete molt occurred roughly in the same period as other dates in the column but without any possibility of fixing a date of inception. Evidence in these instances was derived from a conspicuous shift from totally worn remiges to new ones and in females by the refeathering of a brood patch. In the latter connection we have abundant evidence that a brood patch refeathers only at the time of the general molt. In the interval between molts it may undergo several alternating periods of activity (edematous state) and inactivity but not refeathering.

The interval between initiation of molts averages 165.4 days or about 5 months and 15 days. Extremes are 138 and 190 or about 4⅔ months to 6⅓ months. It is to be noted that all but two of the records are for the interval between a January-March inception and a July-September inception. We may expect that similar records between July-September and January-March would average a little greater, probably about 190 days. Thus there is indication that the year is not divided quite equally. Further evidence in support of this is supplied in figure 3, and the implications of it are discussed in relation to rainfall (p. 155).

The reason for this species having two complete molts a year is not because of the

impact of the double breeding cycle, for the two are not tied together rigorously in a physiologic sequence. However, ecologically there is an apparent reason for the evolution of such a dual molt program. The birds forage in coarse, perennial grasses and the plumage becomes heavily worn in an interval of 5 to 6 months even if the bird has not engaged in the work of feeding a normal, successful brood of one or two young. In some individuals the wing and tail become so abraded that the birds experience obvious difficulty in flight. It was quite evident to us in watching and handling the species that if a year had elapsed between complete molts, the birds would have become incapacitated. The peculiar double molt schedule appears then to be one necessary for survival under the mode of life of the species in this area.

DEGREE OF CORRELATION OF MOLT AND REPRODUCTIVE CYCLE

Female.—The reproductive cycle of the female shows a simple relation to the molt cycle consisting of mutual exclusiveness. The state of reproduction in females was judged only by the presence of an active, edematous brood patch or the presence of an egg in the duct which was evident by an external bulge coupled with a loosening of the cloacal sphincter. Such females were classed as nesting or breeding. All others were regarded as nonbreeding. An inactive brood patch or lack of any bare area could be associated with the nest-building stage and an inactive patch could of course be present when nestlings were in the last half of their nestling period at 7 to 12 days of age.

Few laparotomies of females were undertaken. We are not sure that the ova reduce below 1 to 1.5 mm. in diameter in a nonbreeding interval and their substantial increase above this level would be in a brief period, perhaps 10 days, preceding laying. Thus seldom would worthwhile evidence be derived by laparotomies of this sex where we were dependent to considerable degree on chance in the time of recapture of free-living birds.

From the records of trapped females and those collected for tissue samples, 29 instances of birds with active patches and/or laying can be listed in which data on plumage are explicit. These 29 instances contain no duplications of the same breeding or laying period of a given female. Of the 29, 28 show no molt. The other bird is in molt stage 1, meaning only that body feathers and no remiges were involved. Furthermore it was not at the laying stage. Another individual had an asymmetrical molt of a few inner primaries accompanied by no activity in the other wing or elsewhere on the body. It must be regarded as an accidental feather replacement due to extraction of feathers rather than to true molt. An additional 27 records of females show molt, from stages 2 to 11. All of these birds had either no brood patch or an inactive brood patch at the time.

Thus there is a near-perfect negative correlation between molt and the active laying and brooding period of females. The single exception involves only the earliest stage of molt and may well represent an individual in transition, just at the conclusion of a brooding period. This fact, coupled with evidence of arrested molt (p. 154) associated with breeding in a female, strongly indicates in this sex that the two processes at their peak level are physiologically incompatible. There is an obvious "competition" for nutrients by the two processes in the female. It may be noted that the males do not incubate or brood and thus have neither the energy drain of egg production nor that of brooding. Indeed many, but not all, males take no part in bringing food to the young.

Male.—The male cycle as reported earlier (1959) can be ascertained principally in two ways, by laparotomy and by measurement of the cloacal gland or protuberance. If the testis measures 7 or more millimeters in total length, it is in full reproductive state with mature sperm present. Testes 6 mm. long often possess sperm also but in some they may not yet be quite fully functional. Testes 2 to 5 mm. in length are in various re-

gressed stages or are progressing in recrudescence toward breeding. The decline is very rapid so that the intermediate stages measuring from 3 to 5 mm. probably almost always represent regrowth and progressive stages in maturation of germ cells. For purposes of this study of molt correlation, then, testes 7 mm. or over represent the breeding plateau which is of 3½ to 4½ months' duration, and measurements from 2 to 6 mm. represent regression and recovery, chiefly the latter, with 6 mm. conservatively rated as just short of breeding. The regression and recovery period averages about 2 months, varying from 1½ to 3 months. Moreover the invariable association, in over 100 instances, of a large, 7+ mm. testis with a cloacal protuberance 6 mm. or more in diameter means that a breeding state of the testes can be assumed from such external evidence; probably a protuberance 5 mm. in diameter reflects this level but one or two possible exceptions led me to set the 6 mm.-level as more reliable.

Testis Length (mm)

Molt Stages	2	3	4	5	6	7
no molt		4	1	4	3	65
1		1			1	4
2		1				4
3	2	1			1	4
4						2
5	1				1	
6	2	2			1	
7			1	1		
8						1
9	1	1				1
10		3	1	1		1
11	1	2	1		1	2

Total in molt = 47

Fig. 2. Correlation chart showing relation of breeding state to molt in males of *Zonotrichia capensis*.

The combined evidence on breeding state and molt status is shown in a correlation chart (fig. 2). In this the breeding stages range from testis lengths of 2 to 7 mm., the latter alternatively being indicated by the cloaca, and molt stages are the units already standardized from 1 to 11. Since a testis of 7 mm. normally is sustained for 8 months out of the year in each individual and lack of molt similarly prevails for 8 months, and whereas each molt stage has an average duration of only 6 days, refined statistical manipulation of these data on correlation would be unsound.

There is nevertheless evident a partial inverse correlation. The imperfection of it is obvious from tracing the record of testis stages of 6 and 7 mm. At least occasional molt of all stages except no. 7 can occur in combination with testis 6 or 7 mm. The lack of evidence for molt of stage 7 coupled with enlarged testes may well be a gap owing to sampling. Still the chart does show that the middle stages of the molt process, from 5 to 7, when perhaps the greatest demands are put on the bird for feather growth, are rarely associated with breeding state. Note also that there is a lack of instances of fully reduced testis when no molt is in progress.

The partial exclusion of one state by the other is further reflected in these facts. Of the 47 cases of molt tabulated, one third or only 15 should by chance alone coincide

with a stage of regressed testes (1 to 6 mm.) since both these aspects of the cycles each occupy only a third of the bird's year. As a matter of fact, however, 28 rather than 15 are in regression or recovery phases of the testis cycle. Conversely 40 individuals submaximal for testis should have about 13 in molt stages whereas 28 are in molt.

In the large group of 77 records in which no molt occurs, a status that prevails on the average for 8 months in the year per individual, one would expect that regression, which occupies 4 months' time, should show up in 17 of them if randomly distributed. In fact it occurs in but 12.

Four case histories of adults that are reasonably complete throw further light on this matter. No. 478 on February 14 was in molt stage 5 with testis at 6 mm.; on March 9 it showed molt 8 and testis 7 mm. with obviously no testis recession intervening between molt stages 5 and 8; yet in a later molt, on September 7 it was in stage 10 with testis 2.9 mm. and in a still later molt on January 16, it was in stage 3 with the testis at maximum. Thus even in one individual the processes do not correlate in just the same way from one molt to the next.

No. 472 on July 16 and 19 was in molt stage 2 with maximum testis; on July 19, molt 3 and testis 7 mm. were recorded; August 23, molt 10 and testis 2.8 mm. This type of case history is probably rather frequent with regression during the latter part of the molt.

No. 495 had a somewhat abnormally protracted molt during which a complete regression and recovery of the testes took place. On February 26 and March 4 it was in molt stage 4, but one in which body molt was just then starting, and the testis was 7 mm.; March 27, molt 6 and testis 3.3 mm.; May 8, molt 11 and testis 6+ mm.

No. 806 on March 8 had no molt but the testis was 2.9 mm.; March 25, molt 6; April 24, molt 9 and testis 7+ mm. This bird, like the preceding, had clearly recrudesced in the latter half of the molt.

Discussion.—In summary it should be stressed that molt in adult males does not interfere in all instances with the testis cycle or the converse. The two do have an influence on each other, regressed periods corresponding with molt much more often than would be true by chance alone. The fact that females avoid coincidence of molt and the nesting cycle is not incongruous with the imperfect inverse correlation in males, because it should be realized that the male has long plateaus of breeding potency and the female short periods of actual reproductive activity. A mated pair may spend many weeks together with the male at its high reproductive plateau and yet engage in no nesting. This was particularly true in a well studied pair, ♂460 and ♀488, which was watched almost daily. The male was at breeding state and singing heavily from May 4 to at least July 29 and yet only one nesting was undertaken, with eggs laid on June 8; this nest was successful.

Although males are somewhat more active in territorial defense and singing during their high plateau than at other times, they are not putting out the effort that the female does in brooding, nor in many instances in the gathering of food for the young. Also only two eggs are laid and rarely does more than one young reach the stage of freely following about after the parents subsequent to leaving the nest. Thus there is less competition for energy between the breeding activity of the male and the molt than in the female, or it may be said that his breeding activity load is spread widely so that competition with molt is slight. Compared with north-temperate relatives the male's breeding activity never reaches so sharp a peak as that entailed in simultaneous population-wide territorial establishment and strife and in the frequent feeding trips by both parents necessary for a large brood of nestlings.

ARRESTED MOLT

Four instances came to notice of adult molt that started and then ceased at an early stage coincident with breeding. Three males and one female were involved.

No. 460, a male, on February 10 was in early body molt and primary 1 had dropped and was in a 2 cm. sheath; it was thus in molt stage 2. It had a mate and nest in which eggs had been laid about January 30. On March 6 and 8 there was no molt and the preceding activity had stopped at stage 2. Then on May 4 it was in stage 11, just completing the arrested molt. From February 12 on to March 15 it had engaged in feeding juveniles, in and out of the nest, and on March 26 it was seen at a distance to be molting.

No. 480, a male, started body molt normally in the center of the back on July 30 and thus was in stage 1. Its female had a nest and eggs at that time, the eggs having been laid about July 22. This set did not carry through to hatching, but the male evidently suspended its molt. On October 20 this male was again in stage 1 with reactivation of further replacement in the centers of the spinal and sternal tracts.

No. 484, a male, was at stage 1 of molt on July 8 and the cloacal protuberance was maximum. On July 23, it was in arrested molt at stage 2 and the cloaca was maximal. On August 26 it had obviously resumed molt, as judged from appearance at a distance, and on November 3 it was in stage 11 at the end of this molt.

No. 483, a female, was in stage 1 on July 14 following a laying estimated to have occurred on June 29. On July 16 she was in stage 2 and the brood patch was refeathering. On July 28 she had a new active brood patch and molt had been arrested at stage 2. The molt must have resumed soon after, as it was in stage 11 near completion on September 20 and was entirely finished on October 3.

In each of these histories the correlated breeding conditions or nesting activity strongly suggest that these actively suppressed the molt. There must be some physiologic mechanism for this in both females and males even though it clearly does not always operate in males as the imperfect correlation of molt and breeding in this sex shows. The intervals of suspension of the molt in these four cases seemed to be approximately 20 to 80 days in the males and about 15 days in the female.

ANNUAL OCCURRENCE OF MOLT IN THE POPULATION

Inasmuch as the two complete molts of each adult tend to fall during non-reproductive states of the individual, it follows that on a population-wide basis molt is encountered in two principal segments of the year and that these occur chiefly when nesting is at its lowest levels. What we were not prepared to find was that these two molt periods show sharper "peaking" than do the major nesting periods for the population and that there is a more evident coercion of the molt cycle by the environment than in the case of the breeding cycle.

Figure 3 shows a plotting for a 12-month period of the recorded stages of molt derived from all individuals handled or taken as specimens and from those observed in which obvious, heavy molt was in progress. There are 135 molt records thus involved. There is no duplication of individuals within each 10-day period of the chart except that if the same individual showed two different numbered molt stages when in hand in these 10 days, each is plotted; there are only 5 instances of this. The reciprocal situations where a positive record of no molt was entered for birds examined in hand is shown at the top; there are 144 such positive records. One would expect twice as many non-molt records as molt records for the year; the discrepancy from this expectation is due to failure to record the negative evidence of lack of molt and the fact that absence of molt could never be recorded by observation at a distance to balance the distant visual recording of molt.

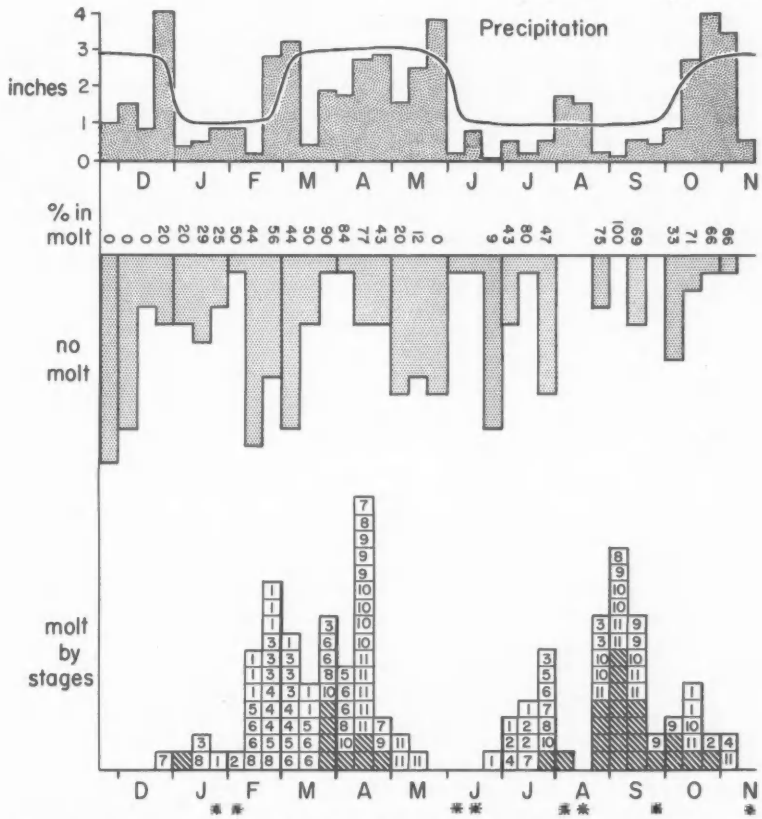
Precipitation
inches
4
3
2
1
0
D J F M A M J J A S O N
% in molt
0 0 0 20 20 29 25 50 44 56 44 50 90 84 77 43 20 12 0 9 43 80 47 73 100 69 33 71 66 86
no molt
molt by stages
D J F M A M J J A S O N

Fig. 3. Seasonal occurrences of molt and molt stages in a population of *Zonotrichia capensis* in correlation with rainfall. Data derived from records at 4 kilometers northwest of San Antonio, 6500 feet, Valle, Colombia. For explanation, see text. Cross-hatched squares indicate birds observed from a distance to be in general molt. Stars indicate 10-day periods in which, due to our absence, few or no data were obtained.

Figure 3 clearly demonstrates that there are two well defined seasons of molt, one from February through April and the other from July through October. There was no evidence whatsoever of adult molt from May 12 to June 25 and similarly none from November 4 to December 20. On the other hand, non-molting birds are recorded for every month and in every 10-day period except those when we were absent or worked at the station only one or two of the 10 days. A total of the individuals recorded with respect to molt or its absence in any 10-day period may be approximated by adding the columns in the two segments of the graph; from this may be figured the percentage of the sample in molt. This is shown at the top and is another reflection of the two definite periods of the year when most molt occurs.

In contrast with the annual distribution of dates of completed sets of eggs (Miller,

MS), the data on molt occurrence show the two gaps just referred to above, each of about 6 weeks' duration. Gaps in nesting occurrences in no instance represented more than single 10-day periods during the "lows," and these can be ascribed to sampling. In general, nest starts varied in the proportion of 1 to 5 between low and high periods, whereas molt comparably varied from levels of zero to 10 or somewhat above.

Figure 3 also reflects by means of the recording of molt stages the expected general, but imperfect, progression of the population from early stages to late stages in each molt period. Thus in the July to October molt, stages 1 to 5 dominate in July but in September stages 8 to 11 prevail. The February to April molt shows the same thing quite as distinctly. Thus this circumstance makes it clear that the curve would have evened out in August if data had been available and that molt must have been extensive in that month; we were absent from the station for almost all of the first 20 days of August.

CORRELATION OF MOLT AND WEATHER

The correlation most obvious between molt and weather is with the rainfall, which although erratic, shows two high and two low periods annually. Our weather data for the one year (fig. 3) do not necessarily represent the average rainfall pattern, although local accounts of wet and dry seasons and data from lower elevations, as at Cali, support the view that the year we experienced was broadly representative. Two conspicuous cessations of frequent, nearly daily, heavy rain occurred—one precisely at the end of May and the other at the end of December. The conspicuous upswing in molt began at a time 3 or 4 weeks later in each instance, even though these events were not quite evenly spaced at six-month intervals. Since molt when once started seems to go through to completion at a rather fixed rate, except for occasional arrest by nesting, the initiation of this physiologic process seems to be most critical and the environmental stimulus for molt control is properly to be sought in association with it rather than with subsequent molt rates and environmental events prevailing during middle and later stages.

Associated with each cessation of frequent rain is an increase in average daily maximum temperature of about 1.7 degrees F. This is of course a small differential and the absolute values for the two molt-initiation periods are in fact 3.8 degrees different (see Miller, 1959:table 2). Still the temperature shift does reflect at our station an even greater increase in the period of the day when the sun is out. The diminution of rains also means substantial periods of each day when the grass is free of drops of water, even though it is wet by precipitation or dew each morning and evening from the almost nightly fog or cloud cover.

If the molt is triggered by the cessation of frequent rain, we are at this stage of our knowledge uncertain whether this is (1) a behavioral and activity response by the bird to stoppage of actual precipitation; (2) the effect of small increase in the temperature itself experienced during the day, but not an absolute temperature level or nighttime temperature change, (3) the changed condition of wetness in the grass in which the birds forage and to which they may react psychologically, or (4) the greater clearing of the skies and the exposure to sun which results. I am inclined to favor the last two possibilities, perhaps in combination, which the bird responds to psychologically with ultimate effect therefrom on endocrine and metabolic balances. The grass itself, it should be understood, never dries out in this area, but remains green, and there is always seeding of the grass, although possible seasonal fluctuations in amount of this were not investigated. The grass is wearing on the plumage at all times.

Frequent although not invariable occurrence of nesting prior to the molt might be thought of as leading to an especially worn state of plumage which stimulates molt, but

in this connection it should be realized that the small broods and widely spaced nestings of a pair do not produce the striking peaks of plumage wear we associate with northern passerines. Moreover there are many cases in which molt starts while young are in the nest and others in which it is delayed for many weeks after one or more nesting efforts. Also it should be recalled that some males do not participate at all in feeding the young.

Apart from the controlling stimulus of the initiation of molt, it should be observed that the population on the average has by this stimulus achieved a schedule in which molt occurs chiefly in the drier seasons and fresh plumage is provided for the ensuing wet seasons. This may have some general advantages, although we have not seen these sparrows badly water-soaked from periods of heavy downpour.

AGE OF INITIATION OF COMPLETE MOLT

Case histories of nine young birds provide the basis for determining age when the first adult molt occurs following the postjuvenal molt. These birds were all handled in the juvenal plumage or at a stage in the postjuvenal molt which permitted a close estimate of their age. Subsequent capture then showed them in some stage of the first adult molt and from knowledge of the time involved in such a molt, that is, two months, the approximate age of initiation of it was established. The figure for age thus derived of course lacks precision, but it probably is within two weeks of the true value. Two of the nine had obviously completed a molt recently, judged by the fresh condition of the remiges, and their age for initiation of the first adult molt can be stated only as possible maxima. It should be noted that no evidence has ever been obtained to indicate that the remiges, other than the inner secondaries are molted in the postjuvenal molt, and therefore in the subsequent three or four months a condition of wear of the juvenal remiges permits determining that the first adult molt has not occurred.

The recorded ages for stage 1 of the first adult molt are as follows, in months: 6¼, 7, 7½, 7½, 8½, 8½, 8¾, no more than 5¾, and no more than 8½. These ages, ranging essentially from 6 to 8½ months, represent molts initiated 2 to 4½ months following termination of the postjuvenal molt, since the latter event occurs at about 4 months of age. The average interval of 3½ months is thus the same as that between adult molts.

In the interval between postjuvenal and first adult molts, the bird, of whatever sex, may attain breeding condition or not. Some that do reach this condition actually engage in nesting. Such was true, for example, of one of the females that had her first adult molt start at 8½ months.

The first molt following the postjuvenal molt is ordinarily a complete molt involving all remiges and the primary coverts as is true invariably of subsequent adult molts. However, some birds in the first adult molt fail to molt the primaries, their coverts, and secondaries 1 to 6. Among the 9 case histories mentioned and 8 skins of immatures (skull evidence of age of 6 to 8 months), 14 showed sure evidence of a complete molt that involved the remiges. Two of the 17 had had incomplete molts and were retaining juvenal remiges and a third, represented by a skin, probably was doing so. A rough estimate of the frequency of completeness of the first adult molt is, then, 80 per cent.

THE POSTJUVENAL MOLT

This partial molt, in which the juvenal patterning, and especially the ventral streaking, is lost, is an important series of changes which aids in estimating the age of an individual. In the early stages of this molt estimates of age are accurate to about 10 days. Preceding the molt, the time required for full growth of the juvenal remiges and rectrices is a reasonably constant period except in obviously sick or runt individuals.

Based on data from the vigorous growth of three hand-raised nestlings, of two broods, which accorded closely with a few case histories of wild juveniles traced from early nestling stages on, a chronology of stages may be established (table 6).

At the conclusion of the growth of the juvenal plumage at about 50 days of age, the postjuvenal molt may begin, but normally it starts after a short interval. We have two

TABLE 6

CHRONOLOGY OF EVENTS IN DEVELOPMENT

Age in days*	Events and stages
12 ± ½	Hatching
21 — 24	Fledging
28 ± 1	Rectrices 32 mm. long
33 ± 2	Rectrices 45 mm. long
40 ± 3	Rectrices essentially full length (52 mm. ± 2), but sheaths present at bases of both rectrices and primaries
45 ± 3	Sheaths at bases of rectrices only
50 ± 5	No sheaths on rectrices (approximate end of dependency)

*Age is from beginning of incubation, which coincides with completion of the two-egg clutch.

clear cases of juveniles starting this molt in the center of the breast and back while still showing sheaths on the rectrices and probable traces on a primary (45–48 days). However, the interval normally is none (without overlap) to 11 days. Fairly certain individual records are as follows: 0, 0, 0, 3, 4, 5, 5, 6, 7, 7, 8, and 11 days. Doubtless there are occasional long retardations, but the normal interval is about 5 days and in estimating age the interval of 5 days may be used. Accordingly the postjuvenal molt may be said to begin at ages from 45 to 60 days, and 54 days is regarded as approximately the modal time for this event.

The time involved in postjuvenal molt must be estimated from a series of stages in the completion of the body feather replacement since the remiges are never molted in more than accidental or sporadic fashion and the rectrices are only involved in part of the cases. The stages employed for the body are the same as the five stages for this process in the adult molt and the spread of the molt through the tracts is similar.

Duration of the postjuvenal molt, judged from adequate histories in which details were recorded, is probably rarely less than 60 days. About eight case histories, most of them running from stage I or II to completion or from stage I to late stage V, indicate two months are occupied; actually most of these would probably require for absolute completion about 70 days. There is one instance of a bird occupying only 30 days from stage II to completion and another that went from I to IV in 32 days. Probably these two individuals completed the process in 50 days. There were two other histories when the molt must have occupied 91 days and 100 days, at least. A range of 50 to 100 days is thus shown and a normal of 70 days indicated. Probably most cases fall in the range of 60 to 80 days. Compared with the adult molt, the normal duration of the incomplete postjuvenal molt is about the same, but the variation in span is almost twice as great.

The age at which young birds complete the postjuvenal molt accordingly is about 4 months. It may rarely be 3 months, as was true in one case (no. 486) where the history from stage II was known; this was the individual that passed from stage II to completion in 30 days. Unless there was an unusually long interval between growth of rectrices and stage I, this bird was indeed rapid in attaining full adult plumage. One female that completed the molt at 4½ months had an active brood patch at 5½ months, and thus was nesting and must have started nest building at close to 5 months of age. On the other

hand, the two individuals with long-protracted postjuvenal molts must have completed them at ages of 5 months or a little more.

The postjuvenal molt in no instance discovered by us involved a regular sequential replacement of the primaries or of secondaries 1 to 6. In 56 birds in stage III or later of the postjuvenal molt or in which this molt recently was completed, there was no instance of orderly molt of these feathers. The same may be said of the greater primary coverts although these coverts were not always specifically checked and the juvenal and replacement feathers of this series are not readily separable on the basis of color. Four instances of replacement of single primaries and two of a single outer secondary were recorded, but the fact that these were odd replacements, occurring only in one wing, indicates they were fortuitous.

In contrast, the inner secondaries, 7, 8, and 9, in four instances were undergoing molt on both sides and since these feathers are often associated in molt with the greater secondary coverts, these cases seem to reflect a true molt. We have no accurate estimate of the frequency of inner secondary replacement in the postjuvenal molt. Probably it occurs in no more than 10 to 15 per cent of the population.

The greater, middle and marginal coverts of the secondary or arm area apparently always are replaced. As in the adult molt this may be early or late in the total process.

The juvenal rectrices were recorded as molted in 9 cases and definitely as retained in 13 instances. Probably there are many more instances of the failure to replace rectrices that went unnoticed, as we often neglected to make a specific record on this score, or the rectrices were worn or wet so that judgment of their newness could not be made. Accordingly the proportion of replacement in the postjuvenal molt cannot be well indicated. Probably it is considerably less than the 40 per cent that the foregoing figures would suggest. It is very likely in the order of 25 to 30 per cent.

COMMENT ON MOLT TERMINOLOGY

It will be observed that names for molt here used for *Zonotrichia capensis* are the same as those in long established usage or represent relatively simple adjustments thereof fitted to the situation. Humphrey and Parkes (1959) in proposing a new system of nomenclature of molts and plumages have sought to overcome some three presumed defects of the terms that are prevalent. First, they seek to have names of the molts always reflect the plumage that is to follow rather than that which is lost. This may have some appeal in logic, but language does not always grow logically and does not have to do so for clear understanding and communication. I have never found new students particularly confused by the terms "postjuvenal," "prenuptial" and "postnuptial" molts. These are obvious descriptive terms even though some relate to loss, partial or entire, of a feather generation and others to the gaining of a plumage.

Second, they seek to divorce terminology from seasonal events or other possibly independent events in the life of the bird. Such a need is partly necessary in tropical species and the situation in *Zonotrichia capensis* is a case in point. But the obviously invariable juvenal plumage needs no replacement in terms, all agree, and I would submit that postjuvenal molt is accordingly the most meaningful and direct description of the molt that follows the juvenal state. It is therefore used here and elsewhere in my dealing with tropical or equatorial birds. I have never found it particularly confusing that some molts are complete and others incomplete and that individuals subsequent to an incomplete molt have a mixture of two or more feather generations. These matters can be readily explained and diagrammed for elementary classes and do not need elaborate explanation or special nomenclature.

Third, Humphrey and Parkes attempt to resolve homologies of the postjuvenal plumages in the situation where some species have one plumage a year and others two alternating plumages by naming one as basic and the other as alternate. This effort and the selection of the word basic is what leads to difficulty and this is pointed up by examples in *Zonotrichia*. In the northern *Zonotrichia leucophrys* and *Zonotrichia atricapilla* the first plumage after the juvenal would be called "basic" by their system as also that of the autumn a year later, with the intervening brightly patterned but non-sexually dimorphic plumages that serve the nuptial functions called "alternate" plumages. In *Zonotrichia capensis* there is then no "basic" plumage, a situation that to this author seems most anomalous from what is implied by the word. The postjuvenal, highly patterned plumages of *capensis* used during nuptial activities are the obvious homologs of the "alternate" plumage of the other *Zonotrichias*. This is in fact the stable and one could say basic plumage of the species and the genus. Why not merely call it the adult plumage as I have done for *capensis*, descriptively, and so also describe the molt which changes it as the adult, complete molt. The meanings seem to be clear and free of ambiguity.

In tropical passerines very generally the postjuvenal, so-called basic plumage is lost or was never possessed, which alternative we do not surely know. The "basic" plumage of Humphrey and Parkes may well then be in them an alternative feature, a retarded type of plumage, added or accentuated in relation to the seasonality evolved in the temperate latitudes. If this follows, their "basic" plumage is the alternate plumage and their "alternate" plumage is the truly basic one. Obviously I do not favor their terms.

SUMMARY

The Andean Sparrow, *Zonotrichia capensis*, at equatorial latitudes undergoes a double molt cycle in a twelve-month period. Two complete, adult-type molts occur, each of about 2 months' duration and spaced at approximately 6-month intervals. The duration of each molt is equivalent to that of several northern passerine species and is shorter than in some tropical and north-temperate types.

The program of replacement in tracts and the duration and timing of molt were ascertained from case histories of retrapped birds, observation of color-banded birds at close range, and prepared study specimens.

Sequence of feather replacement is generally similar to that for north-temperate passerines but greater variability of timing of events within the molt period is evident. Thus the body molt may initiate the molt period or be delayed until the third or fourth primary is dropped, and the replacement of secondary coverts may occur very early or late in the sequence of molt stages defined on the basis of primary replacement.

No instances were found in which adults failed to molt twice in a year. The molt is invariably complete after the first adult-type molt. The first adult molt normally occurs at ages from 6 to 8½ months and 2 to 4½ months after conclusion of the postjuvenal molt. This first adult molt is normally complete, but in two and possibly three out of 17 adequate records there was no replacement of the primaries and outer secondaries.

The terminology of Humphrey and Parkes for postjuvenal plumages as "basic and alternate" is confusing and not usefully applicable in reference to *Zonotrichia*.

The molt season is not sharply defined in the way that it is in higher latitudes, yet most of the population engages in adult molt in a period from February through April and from late July through October. Molt may occur at other times but none of the adult type was found from May 12 to June 25 and from November 4 to December 20.

Correlation of the principal molt periods with rainfall is evident. Molt is probably triggered by the end of the rainy reason or the cessation of more or less daily rainfall.

In the year under surveillance, cessation was abrupt at the end of May and at the end of December. Molt became prevalent in the populations 3 or 4 weeks following such cessation. There were no associated differences in photoperiod or absolute values of temperature. The most likely postulated mechanisms involve either a stimulus to the bird resulting from changes in degree of wetness of the grass in which it forages or one derived from greater periods of clear sky and exposure to direct sunlight. Such stimuli occurring at the end of the rains may actually work in combination to initiate molt.

The postjuvenal molt is always incomplete in respect to replacement of the primaries, primary coverts, and outer secondaries. The tail is molted in about one-fourth of the individuals. The molt normally begins at an age of 54 days from the start of incubation and lasts 50 to 100 days but usually about 70 days.

Postjuveniles terminate the postjuvenal molt at ages of 4 months usually and between this molt and the ensuing first adult molt they may or may not breed. One female is known to have started breeding at 5 months of age.

Molt essentially never occurs in females while they are laying, incubating or brooding, and if they undergo these processes while in molt, the molt is arrested.

The reproductive periods of males, in which the testis is at the enlarged, fully functional level for approximately 4-month spans, occur twice a year. These high functional plateaus of males and their molt periods may coincide. However, there is a partial correlation of regressed testis with molt. The occurrence of molt at this time is about twice as great as would be indicated by chance alone. Thus the two cycles may be supposed to have some influence on each other. Contrasted with females, there is in males less competition for energy between the breeding state and the molting process.

A dual molt program is an apparent necessity in that the plumage of this species in this area, because of its grass-land foraging procedures, becomes worn to a point where less frequent molt would lead to incapacitation.

LITERATURE CITED

Baldwin, P. H.
1953. Annual cycle, environment, and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). Univ. Calif. Publ. Zool., 52:285–398.

Humphrey, P. S., and Parkes, K. C.
1959. An approach to the study of molts and plumages. Auk, 76:1–31.

Michener, H., and Michener, J. R.
1940. The molt of house finches of the Pasadena region, California. Condor, 42:140–153.

Miller, A. H.
1928. The molts of the loggerhead shrike *Lanius ludovicianus* Linnaeus. Univ. Calif. Publ. Zool., 30:393–417.
1954. The occurrence and maintenance of the refractory period in crowned sparrows. Condor, 56:13–20.
1958. Reproductive periods in birds near the equator. Caldasia, 8:295–300.
1959. Reproductive cycles in an equatorial sparrow. Proc. Nat. Acad. Sci., 45:1095–1100.

Pitelka, F. A.
1945. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma*. Condor, 47:229–260.
1958. Timing of molt in Steller jays of the Queen Charlotte Islands, British Columbia. Condor, 60:38–49.

Selander, R. K.
1958. Age determination and molt in the boat-tailed grackle. Condor, 60:355–376.

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RANGE EXPANSION OF THE BREWER BLACKBIRD IN EASTERN NORTH AMERICA

By Lawrence H. Walkinshaw and Dale A. Zimmerman

The Brewer Blackbird (*Euphagus cyanocephalus*) has long been regarded as a western species, a bird typical of much of the United States west of the Mississippi River. It was a common summer resident east to North Dakota and western Minnesota in the 19th century. Blakiston (1862:7) found it breeding in 1858 at the forks of the Saskatchewan River, Saskatchewan, and he recorded it from northwestern Minnesota that year and in 1859 (Roberts, 1932:738). In the same state, Coues (1874:200) found it "breeding abundantly" in the Red River Valley. Roberts (1932:314–315) recorded nests found in Kittson County in 1896 and in Marshall County in 1901. He had written earlier (1914:538) that the species regularly bred "in considerable numbers in *northwestern* Minnesota, especially throughout the valley of the Red River of the North and the region immediately adjacent to the eastward. A few scattered observations confirm its occurrence as a migrant further [sic] east in the state . . . ."

Roberts (1932:314) also described the first nests at Minneapolis which were discovered by F. H. Nutter in 1914. The following year the species was found in Isanti and Sherburne counties. By 1928 it had spread into Carlton and Pine counties, Minnesota, invading the Canadian Zone.

Anderson (1907:306) termed the Brewer Blackbird "a western species . . . a rather rare straggler in Iowa during the migrations, occasionally reaching even to Illinois and Wisconsin."

In the 20th century, particularly since 1925, the Brewer Blackbird has extended its range as a breeding species eastward across Wisconsin, the entire Upper Peninsula of Michigan, the southern part of western Ontario to Sault Ste. Marie, through northern Illinois and northern Indiana, and across much of the Lower Peninsula of Michigan. A similar spread in the nonbreeding season has carried the species to the Atlantic coast and, in winter, to the Gulf states and southeast as far as Key West, Florida.

This paper attempts to document this remarkable expansion of range. We have endeavored to locate all records of the Brewer Blackbird east of the Mississippi River. It is impossible to list them all here, but summaries of records for southern Ontario and the states east of Minnesota are presented. Most accounts of the Brewer Blackbird in the East are based on sight identifications and have been published in the "seasonal record" sections of national, state, and local journals. In order to obtain further details and to provide a check on the published accounts, we have corresponded with many of the original observers responsible for these records, or with persons acquainted with them. Some obviously doubtful records have been encountered; others have proved upon investigation to be unreliable. These are either not cited or are listed with pertinent details. We feel that the great majority of published reports are accurate and that interpreted en masse they provide strong evidence of the change in distribution of the species.

Some records are based on our own unpublished data and on those generously supplied by persons in many states and provinces. The cooperation of these people is gratefully acknowledged. Their assistance has contributed materially to the accuracy and completeness of this paper. For this cooperation and for other courtesies we wish to thank A. E. Allin, J. L. Baillie, L. C. Binford, W. J. Breckenridge, M. Brooks, T. D. Burleigh, L. W. Campbell, B. B. Coffey, Jr., J. B. Cope, Dr. and Mrs. W. P. Cottrille, John Davis, J. L. Diedrich, W. A. Dyer, J. T. Emlen, Jr., J. B. Fleugel, O. J. Gromme, R. Grow, P. Hovingh, Jr., E. E. Kenaga, H. Mayfield, B. L. Monroe, Sr., R. E. Mum-

ford, V. Nolan, Jr., C. S. Robbins, S. D. Robbins, Jr., A. W. Schorger, D. E. Snyder, Dr. and Mrs. J. M. Speirs, R. W. Storer, P. B. Street, J. Van Tyne, H. Wing, and D. W. Warner.

RECORDS INDICATING EASTWARD EXPANSION

The Brewer Blackbird has been collected at least once in each state or province discussed beyond except Maryland, Delaware, Pennsylvania, New York, West Virginia, and Virginia. Sight records for these six states are as follows:

Maryland.—Stewart and Robbins (1958:325–326) term the Brewer Blackbird a "casual visitor" in Maryland, listing six records in 1946, 1951, and 1956, between November 8 and April 8.

Delaware.—Three were seen at Bombay Hook, November 3, 1951 (Potter and Murray, 1955:248). Cutler (1955:34) observed others in the same area between October 24 and December 27, 1953. The species now appears to be a regular visitor in Delaware in winter (P. B. Street, written communication).

Pennsylvania.—One was seen at Lake Ontelaunee, near Reading, on October 15, 1951 (Potter and Murray, 1955:248). A flock of 120 was reported on December 19, 1953, and one female on January 16, 1954, at Exton (Cutler, 1955:35). Maurice Broun saw one at Hawk Mountain, September 29, 1954 (Potter and Murray, 1955:16).

New York.—Two were seen at Monticello, September 26 to October 10, 1953 (Nichols, 1954:9), and one was seen at Jamestown on December 26, 1953 (Baillie, 1954:250).

West Virginia.—Brooks (1958:354) wrote: "The writer has a circumstantial account of a nesting pair of Brewer's Blackbirds near Grafton, W. Va. On May 14, one visited my feeding place in Morgantown."

Virginia.—About 50 were seen on November 26, 1956, at Princess Anne Courthouse (Potter and Murray, 1957:15).

The following accounts pertain to states in which the occurrence of the Brewer Blackbird has been verified by specimens.

Wisconsin.—Kumlien and Hollister (1903:89–90) reported Wisconsin's first Brewer Blackbird nest at Lake Koshkonong on June 14, 1862. They believed the species to be of more regular occurrence in western Wisconsin but reported that F. H. King had rarely met with it in the eastern part of the state.

Schorger (1945:81) listed two specimens taken in Walworth County, on June 6, 1904, and April 14, 1910, but the same author (1934:482) wrote that this blackbird was "rare" in Wisconsin prior to 1926—the year which he considered to mark the beginning of the influx in that state. By 1934, according to Schorger, the species was "a common summer resident, breeding in a narrow area extending from Polk County in the northwest, to Walworth County in the southeast." There were, by that year, records from ten Wisconsin counties, with evidence of breeding from nine (Adams, Dane, Jefferson, Polk, Portage, Sawyer, Walworth, Waukesha, and Wood). By 1954 there were summer reports of the species from more than 30 counties, with published breeding records for eleven. These are summarized beyond.

In Walworth County a male was collected on May 29, 1926 (Ford, 1930:566), and near Madison, Dane County, a nest was found on June 9 of that year (Main, 1926:548). The species was common at Hayward, Sawyer County, in June, 1927, and specimens were collected there in 1929 (Eifrig, 1933: 442). Eggs were taken in Walworth County in 1928, and in 1930 a nesting pair was found in Polk County where 12 pairs bred the following year (Schorger, 1934:482, 484). In 1931 and 1932, Schmidt estimated 500 birds in Adams, Portage, and Wood counties (Schorger, 1934:483). Near Belleville, Dane County, Schorger (*op. cit.*) discovered eight nesting pairs in 1932. The species first bred in Waukesha County in 1933 (Curtis, 1933:142). That year, Walkinshaw observed two birds at Odonah, Ashland County, on June 29. In 1936, he saw a male in Waupaca County on May 29. Three years later Richter (1939:127) wrote that the species was then a summer resident in the marshes near Green Bay. Two pairs appeared at Wind Lake in 1939 (Strelitzer, 1939:109). In 1940, the species was reported from Vilas, Door, and Juneau counties (Barger, 1940*a*:82; 1940*b*:93; 1940*c*:102), and later from Bayfield County (Barger, 1941*a*:45; Feeney, 1942:53). It was subsequently reported from other counties: Brown (Barger, 1941*b*:93), Sauk and Winnebago (Barger, 1946:93), Price (seen

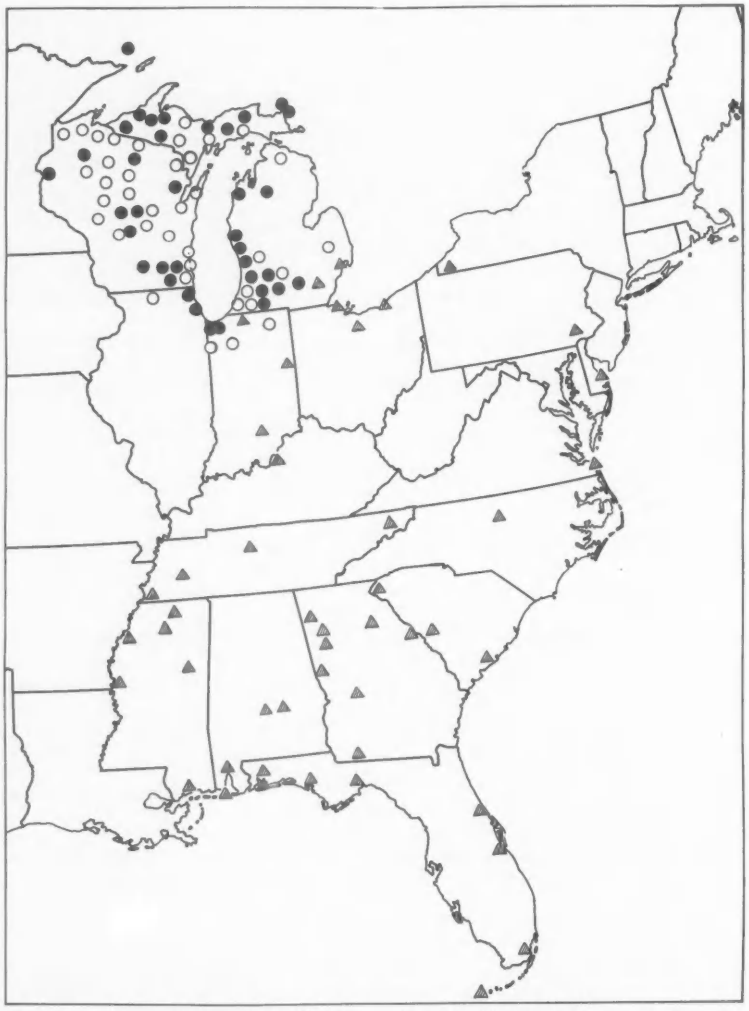

Fig. 1. Recent records by counties of the Brewer Blackbird (*Euphagus cyanocephalus*) east of the Mississippi River. Solid circles designate breeding records; open circles, breeding season records (late May to July); triangles, winter records (late November to February). Map by D. A. Zimmerman.

July 7, 1947, by A. W. Schorger), Taylor and Clark (Robbins, 1947:151), Oneida and Outagamie (Robbins, 1948:122), Jackson, Marathon, Rusk, and Ozaukee (Robbins, 1949*a*:51), Iowa (Robbins, 1949*b*:90), Eau Claire (Robbins, 1949*c*:138), Iron and Waushara (Robbins, 1949*d*:190), Green (Robbins, 1950*a*:142), Columbia and Lincoln (Robbins, 1950*b*:181, 182), Manitowoc and Racine (Strelitzer, 1952:120), Rock (Besadny, 1953*a*:85), Chippewa (Besadny, 1953*b*:141), Marinette and Fond

du Lac (seen June 17, 1953, by J. T. Emlen), Vilas (seen June 22, 1953, by Zimmerman), Dodge (Besadny, 1954:41), and Trempealeau and LaCrosse (Lound and Lound, 1956:184).

In June, 1957, Walkinshaw, Zimmerman, and W. A. Dyer observed Brewer Blackbirds in every northern Wisconsin county traversed by United States Highway Number 2.

Michigan; *Upper Peninsula*.—Blackwelder's (1909:368) early reference to "*Scolecophagus carolinus*" seen along Iron County roadsides during June, July, and August, 1908, probably refers to *E. cyanocephalus*. The birds were seen chiefly in the vicinity of farms. This fact, and the birds' predilection for roadsides, does not suggest the Rusty Blackbird, a species not known to occur in Michigan in summer. However, there was no positive record of the Brewer Blackbird in the state until July 26, 1932, when Wing (1940:193) collected one at Ironwood, Gogebic County. Two years later, on October 3, 1934, M. B. Trautman and G. B. Saunders observed four at Bergland, Ontonagon County. Christofferson (1936:16) saw one at Blaney Park, Schoolcraft County, on October 30, 1935, and he banded one there on October 31, 1939 (notes in Univ. Mich. Mus. Zool.). In 1941, Ammann (1944:48) observed a pair near Crystal Falls, Iron County, on May 1. Near McMillan, Luce County, O. M. Bryens (MS) saw three (including a probable immature bird) on August 10, 1943, and noted others in 1944 and 1945. A pair was reported from near Escanaba, Delta County, in July, 1950 (Gunderson, 1950:277), and on June 17, 1953, J. T. Emlen observed the species there and at Naubinway, Mackinac County. On the same day Walkinshaw, Zimmerman and others found two pairs and a nest at Sleeper Lake, Luce County. Other 1953 summer records include: two at Seney, Schoolcraft County, on June 20 (Walkinshaw, Dyer, and others); a nest at Chatham, Alger County, on June 21 (Zimmerman); adults at Sagola, Dickinson County, and at Arnold, Marquette County, on June 21 (Zimmerman); a nest at Matchwood, Ontonagon County, and eight adults in Gogebic County, on June 21 (Zimmerman); adults near Covington and at Three Lakes, Baraga County, June 27 (Zimmerman).

In 1954, Walkinshaw and R. E. Mumford found three nests and saw ten pairs of birds at Seney on June 23. In 1955, Mr. and Mrs. A. W. Peters found a nest and collected a pair of adults at Ewen, Ontonagon County. Walkinshaw and J. Van Tyne observed nine food-carrying adults near the east branch of the Fox River in Luce County in June. In June and July, 1956, L. C. Binford recorded the species in several different areas: Beechwood, Iron County (nest); Naguanee, Marquette County (female carrying nest material); Channing, Dickinson County; and Greenland, Ontonogan County. Walkinshaw and others found seven nests along the Fox River in Luce County (June 18–19), saw 18 pairs and found three nests in Schoolcraft County (June 25), and noted eight adults and one nest at Kenton, Houghton County (June 21). Binford and Walkinshaw also found three pairs and a nest at Covington, Baraga County, on June 21.

In 1957 and 1958 Walkinshaw and others again recorded the species summering in Luce and Schoolcraft counties east of Seney. In parts of Upper Michigan it is now the most frequently seen blackbird and is fairly common in the nonforested areas.

Michigan; *Lower Peninsula*.—The Brewer Blackbird first appeared in Lower Michigan near Kalamazoo where Fleugel (1948:63–64) saw birds on May 16, 17, and 18, 1947. He found a nest there on June 12 of that year. In the next two years the same observer (written communication) found the species in Van Buren, Berrien, Cass, St. Joseph, and Kalamazoo counties. By 1952, it had spread north during the breeding season to North Muskegon, Muskegon County, where it was recorded in May and June by G. Wickstrom and Walkinshaw.

Searching for the species in 1953, we found it during the breeding season in the following counties: Cheboygan, at Tower, June 28 (one male, Zimmerman); Benzie, at Beulah, June 21 (Hovingh, Ponshair, Walkinshaw), a nest in July (D. Porter), and a male collected on August 1 (Walkinshaw); Oceana, at New Era, June 28, five and a nest (Walkinshaw); Muskegon, at Montague, 18 seen, two collected, and three nests found (P. S. Humphrey and Walkinshaw); Ottawa, in Blendon, Allendale, and Zeeland townships, June 23 and 24 (Hovingh, Ponshair); Allegan, in Heath Township, first seen June 6, 1953, and a nest found July 9, 1954 (Walkinshaw); Calhoun, in Lee Township, May 25 and 27, 1953, three, one collected (Walkinshaw); St. Joseph in Florence Township, adults and young July 19, and a nest on July 21 (Walkinshaw).

We failed to find the Brewer Blackbird in suitable habitat in 24 Lower Michigan counties searched by us in 1953. Except for the single male seen in Cheboygan County, the easternmost breeding season record was from Calhoun County. However, on September 30, 12 birds were observed in Clinton

Fig. 2. Upper: damp field nesting habitat of the Brewer Blackbird near New Era, Oceana County, Michigan, 1953.
Lower: bog nesting habitat of the Brewer Blackbird near the Fox River, Luce County, Michigan, June, 1956. Photographs by L. H. Walkinshaw.

County in south-central Michigan (Wickstrom, 1954:12) and a male was seen on December 27 at Ann Arbor, Washtenaw County, by H. W. Hann (Black, 1954:123).

During 1954, the species again appeared in Allegan County where Walkinshaw observed four on May 9. He found many nests in the course of the summer at Montague and North Muskegon in Muskegon County, and several others in Lee and Marshall townships, Calhoun County. Two migrants or wintering birds were reported by M. Griebe at Rochester, Oakland County, from March 29 to April 1 (O'Reilly, 1956:48).

In 1955 the blackbird appeared in Leoni Township, Jackson County, where C. Haehnle and H.

Fig. 3. Female Brewer Blackbird at nest in leatherleaf bog, Luce County, Michigan, June 22, 1956. Photograph by L. H. Walkinshaw.

Wing saw a male on May 15. Wing and Walkinshaw found a nest there four days later. The species has not yet been found breeding farther east in Michigan.

During 1956 territorial adults were seen by Walkinshaw in Walker Township, Kent County, and nine birds and a nest were found by Walkinshaw in Orangeville Township, Barry County, on June 4. Sight records in fall were made in Lapeer County (single males observed near Imlay City on October 18 and 21 by L. M. and L. P. Zimmerman), and Macomb County (a male seen at Anchor Bay by B. Daubendiek and others; O'Reilly, 1957:2).

Walkinshaw found five birds apparently nesting on May 19, 1957, in Eaton County (T3N, R3W, Section 6). G. Thomas and R. Tompkins found a pair and a nest in Kalkaska County (Section 33) on May 26. Walkinshaw observed 12 adults and collected a female there on May 30, 1957.

The species is not yet known to breed in the extensive muck lands of southeastern Michigan—areas very similar to those selected by breeding Brewer Blackbirds in the western part of the state. However, the easternmost, and most recent, specimen from Michigan was a male found dying of poison at Imlay City, Lapeer County, by L. M. Zimmerman on June 2, 1959. This bird was not fat and its testes were sufficiently enlarged to suggest that it may have been breeding, or about to breed, near that locality.

Ontario.—The first record for this province was that of a male collected by C. E. Hope on June 5, 1939, at Lake Attawapiskat in the Kenora District (Baillie, 1953:307). Subsequently, there were few or no published records until Allin and Dear (1947:175–176) recorded eight, collected a male, and found a nest at Port Arthur in the Thunder Bay District in 1945. E. E. Kenaga (written communication) saw 12 Brewer Blackbirds at Longlac, Algoma District, on September 1, 1948. In 1952, Allin and Dear found a colony in Paipoonge Township. D. Amadon and J. Carleton (Baillie, 1953:307) saw a pair at Garden River on June 17, 1953, and Mr. and Mrs. J. M. Speirs identified a male on September 19 at Echo Bay. At Sault Ste. Marie, between May 18 and June 6, 1954, Mr. and Mrs. Speirs (written communication) found several pairs and a nest. Later in the summer they, with M. Wood, found other nests and discovered a pair feeding young at nearby Echo Bay.

Illinois.—The first record from Illinois of the Brewer Blackbird was made by Ridgway (1889:324) who collected one at Mt. Carmel, Wabash County, in December, 1866. Apparently the species was not again noted in the state until over 60 years later. Lyon (1930:214) reported the first nests on June 17 and June 26, 1929, at Zion, Lake County (Ford, Sanborn and Coursen, 1934:66, recorded the year as 1930). There were several breeding records during the early 1930's and the species persisted in the Waukegan area at least to May 11, 1952 (L. C. Binford).

In Northfield Township, Cook County, Ford (1930:566) observed six pairs and found a nest in June, 1930. During the same month Brodkorb and Stevenson (1934:101) collected a female which contained an egg. White (1935:94) collected a pair near Winnetka on June 15, 1930; he found eight pairs in the same area (Skokie Marsh) in 1931, about 14 pairs in 1932, and 20 pairs in 1933. The colony was reduced to 12 pairs, which moved to a nearby location, in 1934. There were numerous breeding and summer records from Cook County during the 1940's, and the species persists there in many localities to this date.

Mayfield (1949:211) wrote that the Brewer Blackbird was "established as a summer resident" at Rockford, Winnebago County, in 1949. He also mentioned the occurrence of the species in southern Illinois on March 16, 1949. Among the earlier Illinois migration records was that of a male collected on April 9, 1933, at White Heath, Piatt County, by C. R. Naeser (*fide* C. T. Black).

Indiana.—Brewer Blackbirds were first seen in Indiana on April 8, 1949, when R. E. Phillips and others noted them near Schererville, Lake County. The state's first specimen was a territorial male collected north of Ligonier, Noble County, on May 18, 1950, by R. E. Mumford (1950:62–63; 1951: 47). In 1950, the species had been observed at South Bend, St. Joseph County, on March 8 by McErlains, and on May 2 by Dykeman. Binford found the species southwest of Whiting, one-half mile east of the Illinois line, on July 22, 1951, and the same year it was seen again in Lake County. The first Indiana nests were found in Pine Township, Porter County, and in northern Lake County, in 1952 (Mumford, 1954).

On March 29 and 30, 1952, T. Nork, Charles Clark, and others observed two Brewer Blackbirds at Willow Slough Game Preserve, Newton County, where the species has subsequently been seen nearly every spring. Others have been reported during migration in Pulaski and Wayne counties (Mumford, written communication).

Winter records include a male collected by Mumford on January 4, 1954, and one banded and released by Macklin (1954:57) on January 9, 1954, at Bryant, Jay County.

WINTER AND MIGRATORY RECORDS

The Brewer Blackbird has been recorded positively only during migration or in winter from Ohio, Kentucky, Tennessee, North Carolina, South Carolina, Mississippi, Alabama, Georgia, and Florida. Brief summaries of the records known to us for each of these states are given here:

Ohio.—On April 12, 1936, Campbell (1936:452) collected a Brewer Blackbird from a group of five in Spencer Township, Lucas County. On April 3, 1938, Campbell (1939:186) found 55 Brewer Blackbirds in Jerusalem Township, Lucas County, and collected two. The species since has been found occasionally in northern Ohio. Sight records include birds from South Bass Island, Ottawa County, on February 22, 1955 (Nolan, 1955:335); in the Sandusky Marshes on October 20, 1956 (Nolan, 1957: 30); at Cedar Point on February 27, 1954 (Cutler, 1955:35); and at Buckeye Lake on October 20, 1956 (Nolan, 1957:30).

Kentucky.—There are two early sight records from Kentucky: Rowan County, April 9, 1934 (Welter *in* Barbour, 1952:23–29), and Woodford County, May 12, 1938 (Figgins, 1945:300). Ten years later, Monroe and Monroe (1949:73) collected one of eight males which they discovered at Brownsboro, Oldham County, on March 28, 1948. On the same day they collected one of four Brewer Blackbirds from a flock of grackles at Worthington, Jefferson County. Monroe (1957:153; 1958:161) listed the species on Christmas bird counts at Louisville on December 23, 1956, and December 22, 1957.

Tennessee.—Apparently the first record of this species in Tennessee was of one seen April 20, 1935, near Johnson City, Washington County, by Tyler (1935:73–74). Tyler and Lyle (1936:26) reported another there on February 1, 1936.

Burdick (1943:77) observed several on December 11, 1943, near Memphis, and Tucker (1945:58, 60) counted 25 there on December 30, 1945. Coffey (1956:9–10) published numerous winter records, stating that "the species is more frequently seen in November and December . . ." than later in the winter. From March 21 to 23, 1944, Herndon (1950:66–67) reported the species at Elizabethton, Carter County, and F. Behrend reported one from near there at about the same time. Herndon (1951: 18) observed another there on March 13 and 14, 1951. Near Jackson, Madison County, three Brewer Blackbirds were shot from a flock of 2700 otherwise unidentified blackbirds on December 29, 1952 (Roever, Roever, and Shaw, 1952:70–72). Ganier (1957:155) first reported Brewer Blackbirds (110 individuals) from the Nashville area on December 22, 1956.

North Carolina.—South of Asheville, Henderson County, Burleigh (1933:111) collected the first Brewer Blackbird for North Carolina on November 25, 1930. He secured a male and saw a female on April 6, 1931, in Buncombe County. In these two areas Burleigh found the species common in the fall of 1931. On December 22, 1957, Mrs. H. W. Walters observed 800 Brewer Blackbirds at Chapel Hill (Blake, 1958:128).

South Carolina.—Loomis (1887:76) collected three males and two females from a flock of 12 Brewer Blackbirds on December 9 and 10, 1886, at Chester, Chester County, but the species was not again recorded from South Carolina until Sherman and Hudson (1927:567) reported specimens taken on April 17, 1926, and December 18, 1926, at Clemson College, Oconee County. Sprunt and Chamberlain (1949:501) report one taken on November 25, 1932, at Dale, Beaufort County. Post (1951:97) observed three individuals on December 31, 1950, at Aiken, Aiken County, but gave no details of his observation. At Charleston, R. D. Edwards observed 75 birds on December 27, 1956 (Chamberlain, 1957:128).

Mississippi.—Burleigh (1944:464) reported Brewer Blackbirds at Saucier, Harrison County, on December 11, 1935 (one female collected), and he observed the species regularly during the next few winters, collecting several specimens. Burleigh has written us that during the time of his observations, this blackbird "was a common winter resident in Harrison County, flocks of 20 to 100 birds being seen from early November until early April (extreme dates: November 9, 1939, and April 5, 1938)."

At Gulfport, a Brewer Blackbird which was banded May 6, 1942, at Wisconsin Rapids, Wisconsin, was recovered on November 30, 1943 (Searles, 1944:43). At Oxford, Lafayette County, Stevenson (1943:80; 1944:16) observed the species on December 11, 1943, and March 10, 1944. Coffey (1956: 9–10) saw Brewer Blackbirds in DeSoto County on March 8, 1936, and near Lula, Coahoma County, on December 30, 1950 (Coffey, 1951:12). Vaiden (1952:4) reported three sight records, without dates, for the Yazoo-Mississippi delta region, and mentioned Ganier's collection of a female on November 18, 1951, at Grace, Washington County. At nearby Glen Allan, Coffey (1956:10) saw 18 on December 31, 1955. Coffey (*loc. cit.*) cited January records from Oktibbeha and Madison counties in 1954 and 1956, respectively, and Smith (1958:167) reported four seen at Hickory Flat on December 26, 1957. Among the few April records is one of several seen at Greenville on April 3, 1955, by D. and M. Zimmerman.

Alabama.—On March 23, 1936, Burleigh (1936:452–453) collected a female Brewer Blackbird, the first for Alabama, near Foley, Baldwin County. On November 30, 1937, he secured a male and female from a flock of approximately 100 Brewer Blackbirds near Montgomery (1938:545). Near Orion, Ruff (1940:575) observed several individuals on March 16, 1939. Lochridge, Rice, and Summerour (1954:147) saw two on December 31, 1953, at Hayneville, Lowndes County. At Mobile, Dorn (1957:158) observed 250 on December 28, 1956, and Imhof (1957:157; 1958:166) reported small numbers from Dauphin Island in late December of 1956 and 1957.

Georgia.—The Brewer Blackbird was first taken in Georgia by D. V. Hembree, who collected a male on March 1, 1931, at Roswell (Greene, 1934:91). Burleigh (1958:592) lists numerous records for eleven years between 1932 and 1953. Oliver *et al.* (1940:95) report a sight record from Atlanta on December 21, 1939.

More recent records from Georgia include a female found dead in Thomas County on March 25, 1954, and given to H. L. Stoddard (written communication); 620 reported at Rome on December 30, 1956, by Anderson (1957:130); and an estimated 10,100 seen there on December 29, 1957, by Anderson (1958:135).

Florida.—The first record of the Brewer Blackbird in Florida is apparently that of Hallman (1940:574) who collected two birds in Bay County, 20 miles north of Panama City, on December 10, 1939. Burleigh and Lowery (1940:574–575) recorded a flock of eight, two of which were collected, at Vernon, Washington County, on April 8, 1940. In 1941, at Panama City, Hallman secured another on January 30 (Sprunt, 1954:442). No Brewer Blackbirds were then reported from Florida until February 27, 1949, when F. M. Weston saw 50 in Santa Rosa County, 15 miles east of Pensacola (Sprunt, *loc. cit.*). In the same area, Weston observed large numbers of these blackbirds on March 19 and December 10, 1950, and 20 on January 21, 1951. In 1953, Stevenson (1954:15) reported the species on November 21 at Newport, Wakulla County. Stimson (Stevenson, 1954:248) observed four near Miami on January 16, 1954. A small flock which appeared at Key West in October of 1953 built up to about 25 in January, 1954 (Stevenson, *loc. cit.*). The same author (1955:253) reported one seen by several observers at Daytona Beach on December 30, 1954. The species was next reported in 1957: one was observed at Melbourne on January 7 (Stevenson, 1957:262) and a count of 4650 at Pensacola on December 28 (Weston, 1958:144).

GEOGRAPHIC VARIATION IN NESTING HABITATS

Bendire (1895:495) wrote that Brewer Blackbirds nested "mainly in oak, fir, cypress, juniper, pine, willow and apple trees, and in wild-rose, service-berry, and sagebrush thickets. Ordinarily the nests are placed not over 8 feet from the ground, and in certain localities, as near Camp Harney, in southeastern Oregon, they are more frequently placed . . . in the ground, the rim of the nest being flush with the surface." He found "more than fifty" ground nests and noted that "in every case the nest was placed close to or directly on the edge of a perpendicular bank of some small creek . . ."

Dawson (1923:86) cited Bowles' observations of a Washington colony in which, in one season, all nests were at most four feet from the ground in small bushes, and in the next season they were all in cavities in the tops of tall fir stubs, none lower than 150 feet above ground. Dawson (*loc. cit.*) also wrote that "although isolated nests may now and then be found, colonies are the rule; and we sometimes find as high as twenty nests in a single tree, or forty in a given patch of greenery . . . Tyler found [Brewer Blackbirds] breeding at Shaver Lake (elevation 5300 ft.) in the old dead pine stubs standing out in the water."

Williams (1952:3) reported that most of the Brewer Blackbirds in a colony in Monterey County, California, nested in thick tufts of pine (*Pinus radiata*) needles, usually at or near the ends of branches from seven to 43 feet above ground. Occasionally planted cypresses (*Cupressus*) were used. Most nests were from 20 to 30 feet from the ground.

La Rivers (1944:437) listed sagebrush (*Artemisia tridentata*) as the plant most frequently used for nest sites at Reno, Nevada, in 1934. Other plant species which served in this capacity in the order in which they were most used, were *Pinus ponderosa* var. *jeffreyi, Cercocarpus ledifolius, Prunus demissa, Prunus andersoni, Amelanchier alnifolia, Purshia tridentata, Libocedrus decurrens, Abies concolor,* and *Ribes nevadense.* La Rivers found that nest mortality increased from the higher levels to the lower ones (below five feet). The average height of 107 nests reported by him was 5.07 feet (extremes: six inches to 20 feet).

Coues (1874:202) quoted Trippe who referred to Colorado nests "in wet meadows

and brushy swamps . . . placed on any dry spot in the swamp, the centre of a clump of bushes being preferred, and . . . always on the ground."

In western Minnesota, Roberts (1932:315) wrote that this species nested two to eight feet above ground in willows, poplars, or bushes, whereas in the eastern part of the state it nested on the ground in thick grass or under marsh plants. Of 15 nests found in 1942 at St. Paul, four were on the ground; the others were from three to 20 feet high in hedges and trees (Roberts, 1942:10). Formerly only ground nests had been found near St. Paul.

In Wisconsin, Schorger (1934:484) found Brewer Blackbirds nesting on the ground "in dry marshes from which the previous year's growth has been burned . . . nests were found, entirely devoid of cover."

In the Upper Peninsula of Michigan we found the species in wet or damp meadows and fields, along marsh, stream, and lake margins, and in bogs. In a slightly flooded meadow in Alger County, Zimmerman found a nest placed just above the water on a dry hummock. Vegetation surrounding this nest was 25 to 30 centimeters in height and consisted of grasses (*Poa* sp.) and sedges (*Carex* and *Scirpus* spp.) with some buttercups (*Ranunculus* sp.), horsetails (*Equisetum* sp.), and scattered red osier shrubs (*Cornus stolonifera*). In Ontonagon County he found another nest which was well concealed beneath a low *Ribes* plant in a patch of immature goldenrods (*Solidago* sp.). It was on dry ground but only two meters from a water-filled ditch choked with cattails (*Typha latifolia*) and shrubby willows (*Salix* sp.). The first nest found in the Upper Peninsula was in a sphagnum bog at Sleeper Lake, Luce County, and was sunken into the moss under a rather dense growth of cranberry, blueberry (*Vaccinium* spp.), leatherleaf (*Chamaedaphne calyculata*), and other low bog shrubs.

Similarly placed nests were found by Walkinshaw and others in Schoolcraft and Luce counties in bogs east of Seney in 1955, 1956, and 1957. Two others were located beneath very small blueberry bushes about three to five meters from the paved traffic lanes of a state highway. In Houghton County, in 1956, Walkinshaw found two nests in dry fields; one was in a pasture closely cropped by cattle but where several untouched clumps of sedges provided nest sites. The second nest was concealed under a hummock in a grassy meadow.

At Sault Ste. Marie and Echo Bay, Ontario, J. M. and D. H. Speirs found the species nesting in small white spruces (*Picea*) planted along the highway. The nests were close to the trunks and about 2.45 meters above ground. Nests found in western Ontario by Allin and Dear were situated similarly to those found in northern Michigan, being on the ground under grasses or sedges and in or near bogs. Brewer Blackbirds occupy similar nest sites in parts of the Lower Peninsula of Michigan: in Oceana County, Walkinshaw found a nest on the side of a grass-shaded hummock in a dry marsh consisting of sedges, grasses, willows, and goldenrods, and bordered by a grove of arbor vitae (*Thuja occidentalis*). The first nest found in Kalamazoo County, in 1948, was in a similar area.

In southern Kalkaska County, Michigan, several pairs nested on the ground beneath sweet-fern plants (*Comptonia peregrina*), adjacent to a dancing ground of some Sharp-tailed Grouse (*Pedioecetes phasianellus*), on an area managed for that species and burned regularly at two-year intervals by the Michigan Conservation Department. This area was very dry and at least one-half mile from permanent water.

However, the main nesting areas in southern Michigan have been in muck lands, farming regions where the black soil is drained by many small ditches, discharging at the field edges into larger ditches. From these, the water is continuously pumped to keep the soil sufficiently dry to cultivate. Early in the season, in May, nests have been found

beneath the grasses and sedges on the ditch banks, or on unfarmed plots supporting rank growths of grasses, sedges, meadow rue, nettles, goldenrods, and other plants. The areas apparently had been dry marshes, suitable for such birds as the Short-billed Marsh Wren (*Cistothorus platensis*) prior to draining. In places the blackbirds have nested underneath old corn stalks left from the previous season, but in most areas they have nested beneath the growing plants in rows of celery, onions, spearmint, spinach, carrots, or potatoes. Usually the birds have been in loose colonies in certain fields, neglecting other, apparently favorable, fields nearby. The species nested in abundance on muck farms at Muskegon and Montague, Muskegon County, between 1952 and 1955, but from 1956 through 1958, only one nesting pair was found on either of the two areas. Possibly the pronounced lowering of the water table during the latter period was responsible for their absence.

With the exception of three nests elevated a few feet in bushes, found at Glencoe, Illinois, by L. C. Binford, all reported nests in Wisconsin, Illinois, and Indiana have been on the ground.

Many times we have watched breeding Brewer Blackbirds in Michigan feeding at distances of one mile or more from their nesting sites. Usually the birds feed on or along relatively dry ridges such as railroad grades or highway shoulders. When they return to the colony their mouths often are packed with grasshoppers, dragonflies, and other insects. Flight is direct from feeding grounds to nesting areas and both sexes feed the young. Less frequently, the birds feed in the bogs or fields in which the nests are located. Schorger (1934:485) wrote that in Wisconsin the species preferred to feed on cultivated land and always brought food from a distance.

Nests of the Brewer Blackbird vary in structure through the range of the species. Dawson (1923:86) found the interior mould or matrix to be of dry cow dung or mud in California. Some writers have reported that nests appeared like those of crows or jays when placed in trees. In Michigan all ground nests are quite similar to one another. Those in *Sphagnum* moss, in bogs, consist mainly of fine rootlets and grasses, with some coarser materials, such as dead plant stems, between the lining and the moss. These nests usually are sunken to the rim in the soft substrate. The average depth of 19 Michigan nests was 49.9 mm. (extremes: 33 to 61 mm.). The average inside width was 77.3 × 90.8 mm.

NESTING SUCCESS

At Reno, Nevada, La Rivers (1944:436) recorded 205 young maturing from 521 eggs laid (39.4 per cent); young fledged from 53 of 107 nests found (49.5 per cent). On one heavily-farmed muckland area in Calhoun County, Michigan, Walkinshaw found 16 nests of which only two were successful; of 76 eggs laid, eight hatched, and seven young (9.2 per cent) fledged. Two nests were flooded; three were robbed, apparently by Crows, and the remainder were plowed under during cultivating operations. In contrast to this, however, is the high number of successful nestings elsewhere in Michigan. Excluding the single Calhoun County area referred to above, 25 of 32 nests were successful. Of 138 eggs laid, 96 hatched (69.7 per cent), and 77 young (55.8 per cent) left the nests.

SUMMARY

During the 20th century the Brewer Blackbird has extended its breeding range eastward through the Great Lakes region to Sault Ste. Marie, Ontario, and to central, and possibly eastern, lower Michigan. In migration and winter it now appears on the Atlantic seaboard from New York to Key West, Florida. Since the mid-1930's it has apparently become rather regular, and at times common, in the Gulf states in winter.

Between 1914 and 1928, it spread into eastern Minnesota; between 1925 and 1930, across Wisconsin; in 1929 it penetrated into northeastern Illinois; from 1932 to 1953 it spread aross the Upper Peninsula of Michigan, and presumably along the northern shore of Lake Superior in Ontario, reaching Sault Ste. Marie by 1953. In the Lower Peninsula of Michigan it was first found nesting in 1947, at Kalamazoo, and reached northeastern Jackson County in 1955. Although there were but two Michigan records of the species by 1943, a decade later it had become fairly common nearly throughout the Upper Peninsula and was locally common in southwestern Michigan. A specimen collected in eastern Lapeer County, Michigan, in June, 1959, suggests that it now breeds within 40 miles of the southern end of Lake Huron. The first Indiana record, from Noble County, was in 1950; the first nests were found there in 1952.

Nonbreeding individuals were first reported from Ohio in 1936, from Ontario in 1939, from New York in 1953 (no specimens), from Maryland and Delaware in 1951 and 1953, respectively (no specimens). The first specimen from Kentucky was taken in 1948. It was first reliably reported in Tennessee in 1935 and in North Carolina in 1930. Except for a single record in 1886, the first specimen from South Carolina was taken in 1926; the first for Georgia in 1931; for Mississippi in 1935, Alabama in 1936, and Florida in 1939.

That the wintering population in the southeast is composed in part of birds from the eastern sections of the breeding range is suggested by the recovery of a Wisconsin-banded bird in Mississippi.

In northern Michigan, Brewer Blackbirds nest in bogs, wet meadows, and short grass marshes. In the Lower Peninsula of Michigan, most colonies utilize reclaimed muck lands devoted to production of truck crops but near open water. Nests, with few exceptions, are built on the ground. Nesting success in Michigan compared favorably with that in Nevada.

LITERATURE CITED

Allin, A. E., and Dear, L. S.
1947. Brewer's blackbird breeding in Ontario. Wilson Bull., 59:175–176.
Ammann, G. A.
1944. Notes on birds of the Upper Peninsula of Michigan. Wilson Bull., 56:47–48.
Anderson, H. G.
1957. [Fifty-seventh Christmas bird count] Rome, Ga. Aud. Field Notes, 11:130–131.
1958. [Fifty-eighth Christmas bird count] Rome, Ga. Aud. Field Notes, 12:135.
Anderson, R. M.
1907. The birds of Iowa. Proc. Dav. Acad. Sci., 11:125–417.
Baillie, J. L.
1953. [Region reports] Ontario-western New York region. Aud. Field Notes, 7:13–15; 306–307.
1954. [Region reports] Ontario-western New York region. Aud. Field Notes, 8:16–17; 248–250.
Barbour, R. W.
1952. Migration data from eastern Kentucky. Kentucky Warbler, 28:23–29.
Barger, N. R. (editor)
1940*a*. May field notes. Pass. Pigeon, 2:77–83.
1940*b*. June field notes. Pass. Pigeon, 2:91–94.
1940*c*. July field notes. Pass. Pigeon, 2:100–102.
1941*a*. April field notes. Pass. Pigeon, 3:43–45.
1941*b*. September field notes. Pass. Pigeon, 3:92–93.
1946. The spring season. Pass. Pigeon, 8:88–94.
Bendire, C. E.
1895. Life histories of North American birds. Spec. Bull. No. 3, U. S. Nat. Mus.

Besadny, C. D.
1953*a*. The 1953 May day counts. Pass. Pigeon, 15:84–86.
1953*b*. Field notes, the early spring season. Pass. Pigeon, 15:135–141.
1954. Field notes, the autumn season. Pass. Pigeon, 16:33–41.
Black, C. T.
1954. Michigan bird survey. Winter, 1953–54, and spring, 1954. Jack-Pine Warbler, 32:119–134.
Blackwelder, E.
1909. Summer birds of Iron County, Michigan. Auk, 26:363–370.
Blake, C. H.
1958. [Fifty-eighth Christmas bird count] Chapel Hill, N.C. Aud. Field Notes, 12:127–128.
Blakiston, T. W.
1862. On birds collected and observed in the interior of British North America (part 2). Ibis, 4:3–10.
Brodkorb, P., and Stevenson, J.
1934. Additional northeastern Illinois notes. Auk, 51:100–101.
Brooks, M.
1958. [Region reports] Appalachian region. Aud. Field Notes, 12:352–354.
Burdick, A. W.
1943. Notes from the Memphis region. Migrant, 14:77.
Burleigh, T. D.
1933. The present status of Brewer's blackbird in the southeast. Wilson Bull., 45:111–113.
1936. Brewer's blackbird (*Euphagus cyanocephalus*) in Alabama. Auk, 53:452–453.
1938. Second record of Brewer's blackbird in Alabama. Auk, 55:545.
1944. The bird life of the Gulf Coast region of Mississippi. Occ. Pap. Mus. Zool. La. State Univ. No. 20:329–490.
1958. Georgia birds (Univ. Oklahoma Press, Norman, Okla.).
Burleigh, T. D., and Lowery, G. H., Jr.
1940. Brewer's blackbird in Florida. Auk, 57:574–575.
Campbell, L. W.
1936. Brewer's blackbird taken near Toledo, Ohio. Auk, 53:452.
1939. Second occurrence of Brewer's blackbird in Ohio. Wilson Bull., 51:186.
Chamberlain, E. B.
1957. [Fifty-seventh Christmas bird count] Charleston, S.C. Aud. Field Notes, 11:127–128.
Christofferson, K.
1936. Bird observations by members. Jack-Pine Warbler, 14:15–16.
Coffey, B. B., Jr.
1951. The season. Memphis area. Migrant, 22:12–13.
1956. Brewer's blackbirds in the mid-south. Mid-south Bird Notes, 5:9–11.
Coues, E.
1874. Birds of the northwest. U.S. Geol. Surv. Terr., Misc. Publ. 3 (Government Printing Office, Washington).
Curtis, J. T.
1933. Brewer's blackbirds in Waukesha County, Wisconsin. Wilson Bull., 45:142.
Cutler, D. A.
1955. Brewer's blackbird at Bombay Hook, Delaware. Cassinia, No. 40:34–35.
Dawson, W. L.
1923. The birds of California. Vol. 1 (South Moulton Co., San Diego).
Dorn, J. L.
1957. [Fifty-seventh Christmas bird count] Mobile, Ala. Aud. Field Notes, 11:157–158.
Eifrig, C. W. G.
1933. Color of the iris of Brewer's blackbird. Auk, 50:442.
Feeney, W. S. (editor).
1942. The spring season, northwestern area. Pass. Pigeon, 4:50–53.
Figgins, J. D.
1945. Birds of Kentucky (Univ. Kentucky Press).

Fleugel, J. B.
1948. Brewer's blackbirds found nesting in Kalamazoo County. Jack-Pine Warbler, 26:63–64.
Ford, E. R.
1930. Breeding of Brewer's blackbird east of its normal summer range. Auk, 47:565–566.
Ford, E. R., Sanborn, C. C., and Coursen, C. B.
1934. Birds of the Chicago region. Prog. Act. Chi. Acad. Sci., 5:19–80.
Ganier, A. F.
1957. [Fifty-seventh Christmas bird count] Nashville, Tenn. Aud. Field Notes, 11:155.
Greene, E. R.
1934. Brewer's blackbird (*Euphagus cyanocephalus*) in Georgia. Auk, 51:91.
Gunderson, H. L.
1950. [Region reports] Western Great Lakes Region. Aud. Field Notes, 4:276–277.
Hallman, R. C.
1940. Brewer's blackbird in Florida. Auk, 57:574.
Herndon, L. R.
1950. Birds of Carter County, Tennessee. Migrant, 21:57–68.
1951. The season. Elizabethton. Migrant, 22:17–18.
Imhof, T. A.
1957. [Fifty-seventh Christmas bird count] Dauphin Island, Ala. Aud. Field Notes, 11:156–157.
1958. [Fifty-eighth Christmas bird count] Dauphin Island, Ala. Aud. Field Notes, 12:166.
Kumlien, L., and Hollister, N.
1903. The birds of Wisconsin. Bull. Wisc. Nat. Hist. Soc., 3:iv+143 pp.
La Rivers, I.
1944. Observations on the nesting mortality of the Brewer blackbird, *Euphagus cyanocephalus*. Amer. Midl. Nat., 32:417–437.
Lochridge, H., Rice, J., and Summerour, B.
1954. [Fifty-fourth Christmas bird count] Montgomery, Ala. Aud. Field Notes, 8:147.
Loomis, L. M.
1887. On an addition to the ornithology of South Carolina. Auk, 4:76.
Lound, M., and Lound, R.
1956. Field notes. Summer season. Pass. Pigeon, 18:175–184.
Lyon, W. I.
1930. Brewer's blackbird nesting in Illinois. Wilson Bull., 42:214.
Macklin, P. R.
1954. Brewer's blackbird. Indiana Aud. Quart., 32:57.
Main, J. S.
1926. Brewer's blackbird nesting at Madison, Wisc. Auk, 43:548–549.
Mayfield, H.
1949. [Spring migration] Middlewestern prairie region. Aud. Field Notes, 3:210–211.
Monroe, B. L.
1957. [Fifty-seventh Christmas bird count] Louisville, Ky. Aud. Field Notes, 11:153.
1958. [Fifty-eighth Christmas bird count] Louisville, Ky. Aud. Field Notes, 12:161.
Monroe, B. L., and Monroe, B. L., Jr.
1949. Brewer's blackbird in Kentucky. Kentucky Warbler, 25:73.
Mumford, R. E.
1950. Brewer's blackbird. Indiana Aud. Quart., 28:62–63.
1951. Brewer's blackbird in Indiana. Wilson Bull., 63:47.
1954. Brewer's blackbird nesting in Indiana. Wilson Bull., 66:61–63.
Nichols, C. K.
1954. [Region reports] Hudson-St. Lawrence region. Aud. Field Notes, 8:6–9.
Nolan, V., Jr.
1955. [Regional reports] Middlewestern prairie region. Aud. Field Notes, 9:333–335.
1957. [Regional reports] Middlewestern prairie region. Aud. Field Notes, 11:28–30.

Oliver, J. C., Girardeau, L., Gordon,. L., Werner, R. C., Spratt, N., Jr., and Griffin, B.
1940. Bird-Lore's fortieth Christmas bird census Atlanta, Ga. Bird-Lore, 42, suppl. 1:95–96.
O'Reilly, R. A., Jr., (editor)
1956. Bird survey of the Detroit region 1954. Detroit [Mich.] Aud. Soc., 99 pp.
1957. Bird survey of the Detroit region 1957. Detroit [Mich.] Aud. Soc., Vol. 2, No. 1:2.
Post, W., Jr.
1951. [Fifty-first Christmas bird count] Aiken, S.C. Aud. Field Notes, 5:97.
Potter, J. K., and Murray, J. J.
1955. [Region reports] Middle Atlantic coast region. Aud. Field Notes, 9:15–17; 246–248.
1957. [Regional reports] Middle Atlantic coast region. Aud. Field Notes, 11:13–15.
Richter, C. H.
1939. Additions and comments to A. J. Schoenebeck's birds of Oconto County. Part 2. Pass. Pigeon, 1:124–129.
Ridgway, R.
1889. The ornithology of Illinois. Part 1, descriptive catalogue. Vol. 1 (published by authority of the State legislature, Springfield, Ill.).
Robbins, S. D., Jr. (editor)
1947. The summer season. Pass. Pigeon, 9:147–151.
1948. The spring season. Pass. Pigeon, 10:116–123.
1949*a*. The summer season. Pass. Pigeon, 11:44–51.
1949*b*. The fall and early winter season. Pass. Pigeon, 11:80–91.
1949*c*. The late winter and early spring season. Pass. Pigeon, 11:133–139.
1949*d*. The late spring and summer season. Pass. Pigeon, 11:183–190.
1950*a*. The early spring season. Pass. Pigeon, 12:136–143.
1950*b*. The late spring and summer season. Pass. Pigeon, 12:171–183.
Roberts, T. S.
1914. Brewer's blackbird (*Euphagus cyanocephalus*) breeding in southeastern Minnesota. Auk, 31:538–540.
1932. The birds of Minnesota. Vol. 2 (Univ. Minn. Press, Minneapolis).
1942. [The season] Minnesota region. Aud. Magazine, 44, no. 3, sec. 2:10–11.
Roever, K., Roever, Mrs. W. E., and Shaw, J.
1952. [The 1952 Christmas season bird counts] Jackson, Tenn. Migrant, 23:70, 72.
Ruff, F. J.
1940. Brewer's blackbird in Alabama. Auk, 57:575.
Schorger, A. W.
1934. Notes on the distribution of some Wisconsin birds. II. Brewer's blackbird (*Euphagus carolinus*) [sic]. Auk, 51:482–486.
1945. Ned Hollister. Pass. Pigeon, 7:78–83.
Searles, C.
1944. Some banding returns. Pass. Pigeon, 6:43.
Sherman, F., and Hudson, G. E.
1927. Brewer's blackbird (*Euphagus cyanocephalus*) in South Carolina. Auk, 44:567.
Smith, R. D., Jr.
1958. [Fifty-eighth Christmas bird count] Hickory Flat, Miss. Aud. Field Notes, 12:167.
Sprunt, A., Jr.
1954. Florida bird life (Coward-McCann, New York).
Sprunt, A., Jr., and Chamberlain, E. B.
1949. South Carolina bird life. Contr. Charleston Mus.:11 (Univ. South Carolina Press, Columbia).
Stevenson, H. M.
1943. Notes from Oxford, Miss. Migrant, 14:80.
1944. The season at Oxford, Miss. Migrant, 15:16.
1954. [Region reports] Florida region. Aud. Field Notes, 8:13–16; 246–248.
1955. [Region reports] Florida region. Aud. Field Notes, 9:250–254.
1957. [Regional reports] Florida region. Aud. Field Notes, 11:257–263.

Stewart, R. E., and Robbins, C. S.
1958. The birds of Maryland and the District of Columbia. N. Amer. Fauna No. 62:vi+401.
Strelitzer, C. L.
1939. June field notes. Pass. Pigeon, 1:109.
1952. The spring season. Pass. Pigeon, 14:113–121.
Tucker, R.
1945. Annual midwinter bird census. Migrant, 16:58–60.
Tyler, B. P.
1935. Observations from north-east Tennessee. Migrant, 6:73–74.
Tyler, B. P., and Lyle, R. B.
1936. Additions to the list of winter birds of north-east Tenn. Migrant, 7:25–26.
Vaiden, M. G.
1952. Some birds of the Yazoo-Mississippi Delta. Migrant, 23:1–4.
Weston, F. M.
1958. [Fifty-eighth Christmas bird count] Pensacola, Fla. Aud. Field Notes, 12:144–145.
White, J. S.
1935. Further notes on Brewer's blackbird (*Euphagus cyanocephalus*) breeding in northeastern Illinois. Auk, 52:94.
Wickstrom, G.
1954. Seasonal records of Michigan birds. Fall 1953. Jack-Pine Warbler, 32:3–14.
Williams, L.
1952. Breeding behavior of the Brewer blackbird. Condor, 54:3–47.
Wing, L.
1939 [1940]. Birds of the Upper Peninsula of Michigan. Res. Studies State Col. Wash., 7:163–198.

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FROM FIELD AND STUDY

Relationships of the Falconiform Genus Harpagus.—The neotropical genus *Harpagus* is usually placed with the kites. It is characterized by two "teeth" on the upper mandible. The scientific names of the two species of the genus, *diodon* and *bidentatus*, both reflect this fact. The latter, which is the more widespread of the two, is called the Double-toothed Kite. Such "teeth," which are doubtless adaptations for dismembering food, are not unusual in kites. Thus the species of the Old World genus *Aviceda* have variously one or two such denticles, whereas the American Gray-headed Kite of the genus *Leptodon*, a close ally of *Aviceda*, has one.

Some early authors, such as Sharpe in the "Catalogue of Birds in the British Museum," placed these toothed kites in the Falconidae, but it was soon realized that they have nothing to do with that family.

Harpagus is less obviously a kite than are *Aviceda* or *Leptodon*. In proportions and color it is somewhat like many accipiters. Loye Miller (Condor, 39, 1937:219–221) in a paper on the affinities of *Harpagus* remarked: "the general appearance of the bird when I picked it up was that of an *Accipiter* with an abbreviated tail . . . ." Professor Miller prepared a skeleton of this bird which he compared with those of a White-tailed Kite (*Elanus*), a Cooper Hawk (*Accipiter cooperii*), and a Merlin (*Falco columbarius*). He found *Harpagus* very different from *Falco* in most of the characters compared. On the other hand, in several respects he found the osteology of *Harpagus* more like *Accipiter* than like *Elanus*. These data have recently been used to bring the systematic position of the genus again into question. Hellmayr and Conover (Cat. Birds Amer., pt. 1, no. 4, 1949:32, footnote), although leaving *Harpagus* in the "Milvinae," state: "According to Miller skeletal characters of this form reveal its close kinship to *Accipiter*."

I am not competent to discuss Miller's osteological comparisons in detail but would merely suggest that the similarities to *Accipiter* and the differences from *Elanus* may be superficial adaptations. In one comparison this is clearly stated to be the case: *Elanus* has a type of humerus usual in sailing birds; the other two do not. I feel that if the comparison had been with a kite of more or less similar proportions the results might have been very different. Gurney (Ibis, 1881:118–124) in a paper on *Harpagus* states: "Mr. Ridgway informs me 'it is most nearly related, osteologically, to *Ictinia*.'" The latter, of course, like *Elanus*, is a long-winged gliding kite, but at least it belongs to the same "subfamily" of kites as does *Harpagus*, assuming, as I believe to be the case, that the latter is a kite. In any event, Miller was not at all emphatic about his conclusions. He merely listed certain similarities between *Harpagus* and *Accipiter* without implying that its status was finally settled. Gurney also noted that Nitzsch had found the pterylography of *Harpagus* to be similar to that of *Baza* (= *Aviceda*). In a paper just published, Vesta and Erwin Stresemann (Jour. f. Ornith., 101, 1960:394) state that they found the wing molt of *Harpagus* to be typical of the kites of the milvine group. They also note that Suschkin had reached the same conclusion about the position of the genus in his work on the diurnal raptores.

The "reputation" of *Harpagus* has been influenced by some field notes of the junior author of "The Birds of the Santa Marta Region of Colombia" by W. E. Clyde Todd and M. A. Carriker, Jr. (Ann. Carnegie Mus., 14, 1922:146), where it is portrayed as a very savage little hawk that "feeds entirely upon small birds." We are not told the source of the evidence for this rather sweeping statement beyond the fact that a captive specimen ate small, dead birds. Knowledge of this hawk was enhanced by Laughlin's account (Condor, 39, 1937:137–139) of a pair that nested on Barro Colorado Island, Panamá. He refuted the bird-eating habits and found that *Harpagus* feeds upon large insects and lizards, securing the latter by a chase "up a slanting branch, hopping after it—not flying—with wings spread to maintain balance. This method of hunting, although it looked clumsy, was apparently successful. . . ." I have found four other references to the food of *Harpagus* in the literature or on specimen labels. All refer to insects; one refers also to reptiles.

Mr. Eugene Eisenmann, who has had considerable experience with *Harpagus*, including observations of the pair studied by Laughlin, tells me that small birds usually are unconcerned when a member of this genus is nearby. Wetmore (Proc. U. S. Nat. Mus., 87, 1939:184) was made aware of the presence of *Harpagus* by the alarmed chirping of a large hummingbird, *Cyanolesbia*, and Eisenmann saw one chased off by a pair of Streaked Flycatchers (*Myiodynastes maculatus*). Hummingbirds and tyrant flycatchers are, however, unusually pugnacious birds.

The problem of possible mimicry among birds of prey is one which still awaits clarification. The following paragraph from Newton's article on this subject in the "Dictionary of Birds" (p. 574) is of interest: "On the information of Mr. Salvin, Mr. Wallace has cited (*Contrib. Nat. Select.* p. 107) another very curious case of Mimicry in Birds. This is furnished by *Accipiter pileatus*, a widely-ranging species of Sparrow-Hawk which near Rio Janeiro departs from the plumage it wears in other places to assume that of *Harpagus diodon*, a local species of insectivorous habit, with the object, as suggested, of deluding small birds into the belief that it is harmless in character. The similarity here extends to both immature and adult plumages, which are very different." It should be pointed out that although the adult and immature plumages of *Accipiter bicolor pileatus* are very like those of *Harpagus diodon*, it is not, of course, definite that the former has departed from its usual coloration only in the range of *diodon* or that the resemblance has any special significance. Races of *bicolor* with streaked immatures are found beyond the range of *diodon*; conversely, the northern half of the range of *diodon* has another race of *Accipiter* in which the immatures are immaculate white ventrally and quite unlike those of *diodon*.

A further point is that, assuming there is mimicry involved, we do not know whether the more predatory species (*Accipiter*) is mimicking the inoffensive one (*Harpagus*) or vice versa. As Meyer and Wiglesworth (Birds of Celebes, 1, 1898:66–72, color pls. 2 and 3) state in their lengthy discussion of the remarkable similarity in all plumages between a honey-buzzard kite (*Pernis celebensis*) and the eagle (*Spizaetus lanceolatus*) it is possible that the inoffensive kite might obtain relief from enemies, presumably nest predators, by resembling the eagle. They conclude, however, that both species are so uncommon that it is difficult to postulate mimicry upon any basis whatever.

If *Harpagus* does mimic accipiters, this was of little avail in the pair observed by Laughlin. One of the pair was rather easily frightened from the nest by a toucan (*Ramphastos*) which proceeded to eat the kite's egg!

In summary, one may conclude that *Harpagus* is not related to *Accipiter* and that the resemblance between the two may possibly, although this is unlikely, represent mimicry.—Dean Amadon, *American Museum of Natural History, October 31, 1960.*

Records of the Rarer Native Forest Birds of Kauai, Hawaii.—Delacour in his foreword to Greenway's Extinct and Vanishing Birds of the World (1958:iv) states that "we still know nothing of the . . . status of the rarer birds of the Island of Kaui (*sic*)." However, just as Richards and Baldwin (Condor, 55, 1953:221) rediscovered certain species in remote native forests of Hawaii and Maui, we have been able, with the aid of grants from the McInerny and Castle foundations of Hawaii, to ascertain that all of the native forest birds of Kauai still exist. Nomenclature in the following annotated list follows Amadon (Bull. Amer. Mus. Nat. Hist., 95, 1950:157–262). Except where otherwise noted the species were found only in the Alakai Swamp forest area (elevation 3750 to 4500 feet), the highest mountainous region of Kauai, in July and August, 1960. An asterisk indicates that specimens were collected and placed in the Bishop Museum, Honolulu. Apparently none of these species has been collected since the 1890's.

Thrushes

*Phaeornis obscurus myadestina.** Omao. Several dozen individuals seen or heard. Reported seen in 1941 (Munro, Birds of Hawaii, 1944:77) and heard by Baldwin in 1960 (Elepaio, 21, 1960:2).

*Phaeornis palmeri.** Small Kauai Thrush. At least 15 individuals seen. Listed as probably extinct by Amadon (*op. cit.*:256). Reported seen in 1940 by Donaghho (Elepaio, 2, 1941:52).

Honey-eaters

*Moho braccatus.** Kauai Oo. Twelve individuals seen or heard. This oo, probably the only one surviving of four Hawaiian species, was reported seen in 1936 and 1940 by Donaghho (*op. cit.*).

Hawaiian Honeycreepers

*Loxops maculata bairdi.** Creeper. Abundant; several hundred seen. Reported seen by Munro (*op. cit.*:105) and by Hansen (Elepaio, 20, 1959:10) at Kokee but considered rare.

*Loxops coccinea caeruleirostris.** Akepa. Uncommon; 20 or more, usually widely scattered individuals, seen both in Alakai Swamp area and at lower elevations such as around Kokee. Also reported seen by Hansen (*op. cit.*) at Kokee.

*Hemignathus procerus.** Kauai Akialoa. Two seen, one by David Woodside. Reported seen in 1941 by Munro (*op. cit.*:116) and by Valdemar Knudsen (unpubl.) in 1957.

Hemignathus lucidus hanapepe. Nukupuu. Two seen. Apparently last reported in 1899 (Munro, *op. cit.*:117).

Psittirostra psittacea. Ou. Three seen, two by David Woodside. Reported seen in 1940 by Donaghho (*op. cit.*).

The other native forest birds of Kauai, listed below, were either abundant or reasonably so in both the Alakai Swamp region and the lower, disturbed, native forest. This forest has been altered chiefly by widespread introduced plants such as blackberries and lantana. The Elepaio is an Old World flycatcher (Muscicapidae); the last four species are drepaniids.

Chasiempis sandwichensis sclateri. Elepaio.

Loxops virens stejnegeri. Amakihi.

Loxops parva. Anianiau.

Himatione sanguinea sanguinea. Apapane.

Vestiaria coccinea. Iiwi.

Our studies clearly showed that the rarer forest birds occurred only where the native forest was undisturbed. Steps are now being taken, apparently with the strong support of officials in Hawaii, to set aside an inviolate native forest sanctuary of over 12 square miles encompassing the Alakai Swamp forest area. We hope that here ornithologists will be able to see a variety of unique Hawaiian birds for many years to come.—FRANK RICHARDSON, *Department of Zoology and Washington State Museum, University of Washington, Seattle, Washington,* and JOHN BOWLES, *Punahou School, Honolulu, Hawaii, October 9, 1960.*

Occurrence of the Cassin Race of the Peregrine Falcon in Uruguay.—Hellmayr and Conover (Cat. Birds Amer., pt. 1, no. 4, 1949:297–299) record the race *anatum* of the Peregrine Falcon (*Falco peregrinus*) in Uruguay. However, these authors do not list the race *F. p. cassini* for this country (*op. cit.*: 300–301). Aplin (Ibis, 1894:195) saw examples of *Falco peregrinus* on November 9 and February 8, 1892, in the Departamento de San José, Uruguay. He considered that the form *cassini* was involved in these records. However, the dates of observations during summer in the southern hemisphere make this claim doubtful since the race *anatum* may winter in this area at that time.

In 1957, Mr. Enrique Gomez Haedo sent me two specimens of *F. peregrinus*. Both birds were young females and were shot as they stooped at duck decoys. The locality where they were taken was Coronilla, Departamento de Rocha, Uruguay. This is a region of marshes and lagoons where water birds are plentiful. The specimen obtained on March 31, 1957, is a typical *anatum*. The other, taken on May 18, has a very dark and heavily marked plumage with under parts suffused with deep rufous. I tentatively identified this bird as *F. p. cassini*. In order to check the skin I sent it to the United States National Museum. Mr. Herbert Friedmann confirmed my determination saying "I find that it is *Falco peregrinus cassini*. We have only two specimens of this form in comparable plumage, and your bird obviously agrees with them except that it is slightly darker. Our two birds come from Chile and Bolivia." Accordingly this bird constitutes the first substantiated record of *F. p. cassini* for Uruguay.

I express my gratitude to Dr. Friedmann for help in the identification of this specimen.—RODOLFO ESCALANTE, *Montevideo, Uruguay, September 12, 1960.*

Recent Shorebird Records for Montana.—Just east of the Continental Divide, two miles northwest of Fairfield, Teton County, is a large irrigation sump reservoir, known as Greenfields or Freezeout Lake. On May 20, 1960, a flock of about fifteen Black-bellied Plovers (*Squatarola squatarola*), two Knots (*Calidris canutus*), and ten Dunlins (*Erolia alpina*) was observed here for a two-hour period. The Black-bellied Plover has been recorded before as a fall migrant in Montana, but only one spring sight record is available, and this is west of the Divide (Hoffmann, Hand, and Wright, Condor, 61, 1959:148). The Knot is represented in Montana by a mummified carcass from Lake Bowdoin, Phillips County (Wetmore, Auk, 37, 1920:45), and two July sight records from Medicine Lake, Sheridan County (Hotchkiss, Condor, 50, 1948:275), both in eastern Montana. The Dunlin has never before been reported in Montana. A male and female Dunlin, both extremely fat, were

collected and are deposited in the Montana State University Zoological Museum (MSUZ 5914–15), but despite all efforts, no Knots or plovers could be secured.

Although the Western Sandpiper (*Ereunetes mauri*) migrates throughout the western United States, it has never been recorded from Montana. Moreover, the Semipalmated Sandpiper (*Ereunetes pusillus*) has been recorded only as a migrant east of the Continental Divide (Saunders, Pac. Coast Avif., No. 14, 1921:49). This is not surprising in view of their close resemblance to each other and to the Least Sandpiper (*Erolia minutilla*), which would lead to their being overlooked. For the last few years we have suspected that both species of *Ereunetes* migrated through western Montana in both spring and fall, but we hesitated to publish sight records of species so difficult to identify with certainty in the field. The first specimen of Semipalmated Sandpiper from the west, a male (MSUZ 3882), was taken by D. E. Davis at a slough east of Somers, Flathead County, on August 14, 1952. Finally, this spring we succeeded in obtaining a female Western Sandpiper (MSUZ 5913) at a small pond on the south edge of Missoula, Missoula County, on May 17, 1960. This is the first specimen collected and establishes the occurrence of the species in Montana. Selected sight records for previous years include the following: August 8, 1954, two miles west of Missoula—flock of six Western, one Semipalmated and one Least; April 30, 1955, Kicking Horse Reservoir, Lake County —three Western and one Least; May 21, 1955, Kicking Horse—flocks of twenty and of three Semipalmated; August 26, 1955, Kicking Horse and Ninepipe Reservoirs, Lake County—a few Western and Semipalmated in each of several flocks of Least; August 10, 1956, Kicking Horse—a flock of more than twenty, including one Western, one Baird (*Erolia bairdii*) and several Semipalmated; July 30, 1957, Kicking Horse—flock of fifteen Semipalmated; August 14, 1958, pothole near Ninepipe—flock containing three or four Western, about twenty Semipalmated and four Least; August 14, 1959, south edge of Missoula—flock containing one Baird, two Western, eight Semipalmated and three Least. It appears, then, that Western and Semipalmated sandpipers accompany the more common Least Sandpiper in migration through western Montana, particularly in the fall.

Previous records of the Semipalmated Plover (*Charadrius semipalmatus*) in Montana are all summer or fall sightings. The first specimens have been taken recently and include spring migrants: three males, taken on May 7, 1960, four miles southeast of Frenchtown, Missoula County, on the edge of a water-filled abandoned gravel pit (MSUZ 5919–21); one fall specimen, a female from Lake Bowdoin, Phillips County, on August 27, 1959 (MSUZ 5770). In addition, a single bird was seen on May 20, 1960, at Freezeout Lake.

The Sanderling (*Crocethia alba*) is recorded as a fall migrant both east and west of the Divide (Silloway, Summer Birds of Flathead Lake, Bull. Univ. Mont., Biol. Ser. No. 1, 1901:41; Weydemeyer and Marsh, Condor, 38, 1936:195). On May 22, 1960, three were collected at the gravel pit four miles southeast of Frenchtown, Missoula County (MSUZ 5916–18). These constitute the first spring migration record for the state.—ROBERT S. HOFFMANN, *Department of Zoology, Montana State University, Missoula, Montana,* and RALPH L. HAND, *Missoula, Montana, July 12, 1960.*

Least Flycatchers in Northwestern Washington and Central British Columbia.—On June 21, 1958, while at Ship Harbor, one mile west of Anacortes, Skagit County, Washington, studying Traill Flycatchers (*Empidonax traillii*) under the sponsorship of the American Philosophical Society, we heard a bird which sounded like a Least Flycatcher (*Empidonax minimus*). Michener was the first to hear it singing in the deciduous woods on the southern edge of a large swampy and brushy area where Traill Flycatchers occurred. The understory of the woods was dense dogwood and alder.

This bird was again heard on June 23, when we made a tape recording of its song (cut 3, Cornell Library of Natural Sounds). Playback of songs of a Least Flycatcher, recorded in Freeville, New York, was accomplished by using portable tape equipment and loudspeaker. The loudspeaker was mounted about 15 feet up in a deciduous tree which had been used by the bird as a song perch. The bird responded positively to the playback by approaching the speaker and "singing."

This bird was collected, and the skin deposited at Cornell University. The following data may be found on the label: "original number RCS 58–4, male, testes about 4 mm. long, skull ossified, no fat, weight 10 grams, total length 127 mm., wing spread 197 mm." The following measurements have been made: wing chord 63.5 mm., tenth primary shorter than the fifth, tail 53 mm., bill (nostril to tip) 6.6 mm., tarsus 17 mm. The identification has been verified by John W. Aldrich and Allan R. Phillips.

On July 9 two specimens of Least Flycatcher were taken at Watson Lake, about 5 miles north-northwest of 100 Mile House. The songs of each were recorded. These specimens were taken in the aspen groves on the north side of the lake where about 10 per cent of the wooded area consisted of lodgepole pine. There was very little brush in the understory. One specimen responded by singing with the playback; the other approached the speaker and was observed pumping its tail and giving tail flicks. These specimens were also identified by Phillips. In addition, Least Flycatchers were heard at 124 Mile on July 6 and at Timothy Lake on July 8.

While the species is not listed as occurring in Washington State by Jewett, Taylor, Shaw, and Aldrich (Birds of Washington State, 1953), the species has extended its range in British Columbia, and presumably these observations represent a still farther extension of the range of the species. Munro and Cowan (A Review of the Bird Fauna of British Columbia, 1947) listed the species only for the Peace River Parklands, east of the Rocky Mountains. They indicate that several species of eastern birds pass into the sub-alpine forest biotic area and to a lesser extent into the Cariboo Parklands biotic area. Miller (Condor, 57, 1955:62–63) reported a specimen from Indianpoint Lake in the sub-alpine forest area, which was unknown to Munro or Cowan at the time of their review.—ROBERT C. STEIN and MARTIN C. MICHENER, *Laboratory of Ornithology, Cornell University, Ithaca, New York, December 20, 1960.*

Brewer Blackbird Nesting in Eastern Michigan.—Since 1947 the Brewer Blackbird (*Euphagus cyanocephalus*) has been found breeding in several counties of the Lower Peninsula of Michigan. All these records are from the western half of the state. In Bay County on June 4, 1960, Grefe found a nest of this species which contained four young. On June 13, 1960, Wolf visited the area, which is 7½ miles east and 1½ miles north of Bay City, and collected the adult male and one of the young from the nest. These specimens are now in the collections of The University of Michigan Museum of Zoology. No other nest was found in the area, but four recently fledged young were seen being fed by adults on June 11. Three pairs were seen in the area at one time.

Zimmerman and Van Tyne (Occ. Papers No. 608, Univ. Mich. Mus. Zool., 1959:53) and the A.O.U. Check-list (1957:536) list no breeding records of this species from this far east in Michigan. —LARRY L. WOLF, *The University of Michigan Museum of Zoology, Ann Arbor, Michigan,* and ROBERT E. GREFE, *Saginaw, Michigan, December 18, 1960.*

Occurrence of the Oystercatcher and Curlew Sandpiper in Korea.—On September 10, 1960, I took a single male Oystercatcher (*Haematopus ostralegus osculans*) on a strip of wet mud at the edge of the Han River near the station of Sobbingo on the southwestern outskirts of Seoul, Korea. It was closely associated with another individual of the same species which circled low overhead several times, shortly after the collected bird was wounded. The specimen weighed 403 gms. and was heavily infested with ectoparasites. It was deposited in the Museum of Vertebrate Zoology. Since this is only the second time that I have observed the species during the past seven years of residence in Korea and since, apparently, it has not been collected in South Korea in the past thirty years (Austin, Bull. Mus. Comp. Zool., 101, 1948:108), the present record is of some importance.

On September 11, 1960, Lt. Col. Thomas M. Carson and I took a single female Curlew Sandpiper (*Erolia ferruginea*) that was feeding in shallow water on flooded salt flats along the coast of the Yellow Sea approximately four miles northeast of Inchon, Kyonggi-do, Korea. This is the same area in which I obtained the first Korean specimen of the Temminck Stint (*Erolia temminckii*) on September 29, 1957 (Fennell, Condor, 61, 1959:227–228). It was closely associated with three Little Stints (*Erolia ruficollis*). It weighed 47 gms. and, from the unossified condition of the skull, appeared to be an immature individual. Austin (Bull. Mus. Comp. Zool., 109, 1953:433) and the Ornithological Society of Japan's 1958 "Hand-List of the Japanese Birds" refer to the species as a rare transient in Japan, the latter stating the species was "recorded mostly in May and once in September." Shaw (Zoologia Sinica, 15, 1936:432–433) calls it "not uncommon" as a migrant in Hopei Province of North China, where it passes through in May and September, and he states, further, that "it is also a summer visitor, but not common." Meise (Abhandlungen und Berichte der Museen für Tierkunde und Völkerkunde zu Dresden, Band 18 [1931–34], 1934:72) refers to it as a migrant in Manchuria and lists four specimens taken near Charbin on May 23, 24, and 31. Hachisuka and Udagawa (Quart. Jour. Taiwan

Mus., 3, 1950:142–143) list a total of six specimens taken on Formosa and state that it "is an uncommon migrant among small waders on the China coast; a rare visitor to Japan and unknown to the Ryukyus." Most of the Fukien records, like those of Formosa, were made "between April and June." Although these references show that the species has been recorded from most of the land masses surrounding Korea, in so far as I am able to ascertain, this is the first time it has been collected and recorded in Korea. The specimen has been deposited in the Museum of Vertebrate Zoology. —CHESTER M. FENNELL, *Seoul, Korea, September 24, 1960.*

Two New Records of Birds for California and Notes on Species of the Imperial Valley and Salton Sea Area of California.—*Ereunetes pusillus.* Semipalmated Sandpiper. While examining many dead and dying Least (*Erolia minutilla*) and Western (*Ereunetes mauri*) sandpipers and other shorebirds on a mud flat near the Salton Sea west of Niland, Imperial County, on May 7, 1960, a Semipalmated Sandpiper was found in weakened condition. It proved to be an adult male (testis 2 mm.) in breeding plumage. The specimen is now number 2945 in the Cardiff Collection. At the local headquarters of the California State Division of Fish and Game, I was told that these shorebirds were probably dying from botulism, which is not uncommon along the east shore of the Salton Sea at this season. A Semipalmated Sandpiper was taken on April 23, 1957, at Sasabe, Arizona, about 250 miles southeast of Niland (Levy, Condor, 60, 1958:70) but I can find no records of this species for California.

Sturnus vulgaris. Starling. Starlings were taken on three occasions north of Westmorland, Imperial County, California. An adult female was collected from an eucalyptus tree in a deserted farmyard on February 9, 1957. It was the only one observed. Three specimens were taken from a flock of about 15 at the same locality on November 19, 1957. They were with a large flock of Redwinged Blackbirds (*Agelaius phoeniceus*), Brewer Blackbirds (*Euphagus cyanocephalus*), and Brown-headed Cowbirds (*Molothrus ater*) perched in eucalyptus trees and feeding in nearby fields. A male in breeding condition (testis 12 mm.) was taken northwest of Westmorland on March 21, 1959, near a deserted farmyard. There are other sight records in Audubon Field Notes for this area, but these are the first specimens taken.

Tangavius aeneus milleri. Bronzed Cowbird. On April 22, 1956, I collected a Bronzed Cowbird (no. 2582, Cardiff Collection) north of Westmorland, Imperial County, California. It was a female with the largest ovum measuring 2 mm. It was perched in the top of a dead cottonwood tree in a deserted farmyard. This species was reported from the California side of the Colorado River near Parker Dam several times between 1950 and 1952 (Monson, Condor, 56, 1954:229). This record extends its range about 65 miles farther west.

Junco hyemalis hyemalis. Slate-colored Junco. One was taken (sex unknown) northwest of Westmorland on February 5, 1955. It was with a flock of Oregon Juncos (*Junco oreganus*) along a row of Tamarisk trees. The specimen was examined by Alden H. Miller and proved to be of this race. This is the first record of the race for the Colorado desert.

Melospiza georgiana ericrypta and *Melospiza georgiana georgiana.* Swamp Sparrow. The Swamp Sparrow reported by me (Condor, 56, 1954:54) which was collected on February 1, 1953, west of Niland, was later identified by Alden H. Miller as belonging to the very dark eastern race *georgiana.* This is the first record for this race in California. Two other Swamp Sparrows of the race *ericrypta* were collected in the same area in two separate fresh water marshes west of Niland and north of Westmorland, near the edge of the Salton Sea. One was a male (no. 2162, Cardiff Collection) taken on April 2, 1953, and the other a female (no. 2232) taken on April 25, 1953. Neither bird was in breeding condition. These are the fifth and sixth occurrences for this race of Swamp Sparrow in California and the first records for the Imperial Valley. The specimens were examined by Alden H. Miller.— EUGENE A. CARDIFF, *San Bernardino County Museum, Bloomington, California, September 6, 1960.*

Correction.—In the paper on "Food Habits of the California Quail in Eastern Washington" (Condor, 62, 1960:473–477) an error appears on page 475. The corrected paragraph which begins on the 15th line from the bottom of page should read as follows: "In all, 169 different food items were recorded of which 159 were plant species. Those items found in crops and gizzards in quantities greater than 0.5 per cent of the total volume are listed in table 1 and table 2, respectively. Those found in quantities of less than 0.5 per cent are as follows:".—IRVEN O. BUSS, *Department of Zoology, Washington State University, Pullman, Washington, January 12, 1961.*

NOTES AND NEWS

Dr. Herbert Friedmann of the United States National Museum has been appointed Director of the Los Angeles County Museum. He will assume his duties in Los Angeles on April 1, 1961.

Dr. Oliver L. Austin, Jr., of the Florida State Museum has been appointed by the Nuttall Ornithological Club as chairman of its committee on the Bent Life Histories. He succeeds the late Wendell Taber who had worked with great vigor and excellent results in bringing the life history series near completion.

As a result of a generous bequest from Elsie Binger Naumburg, who, with her late husband, Walter W. Naumburg, founded the Frank M. Chapman Memorial Fund, it is now possible to expand the Fund's program. In addition to cash grants in support of research, ornithological fellowships with a tenure of one year will be awarded. Applicants need not be residents of the United States. It is expected that recipients will carry out research at the American Museum of Natural History, although in exceptional circumstances they might do so at one of the Museum's Field Stations or elsewhere.

Grants will ordinarily be made in March and October, and applications should be in hand by the first of these months. They should outline the proposed research, the applicant's qualifications, provide a budget when necessary, and, for graduate students, include one or two supporting letters. Non-expendable equipment will, at the discretion of the Committee, remain the property of the Museum. If specimens are collected, it is expected that all or some of them will revert to the Museum. A copy of any published result of research supported by the Chapman Fund should be sent to the Chairman, and will, it is hoped, give credit for the aid so received.

Applications for fellowships or for grants in support of research should be sent to the Chairman, Frank M. Chapman Memorial Fund Committee, American Museum of Natural History, Central Park West, New York 24, New York.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the Life Sciences is May 15, 1961. Proposals received prior to that date will be reviewed at the summer meetings of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the May 15, 1961, closing date will be reviewed following the fall closing date of September 15, 1961. Inquiries should be addressed to the Biological and Medical Sciences Division, National Science Foundation, Washington 25, D.C.

The Josselyn Van Tyne Memorial Fund will have a sum of $300 available for research awards at the end of the fiscal year, July 31, 1961. Any student of birds is invited to apply for part or all of this amount.

Ten duplicate copies are desired for distribution to members of the Research Committee who will determine how the funds will be allotted. The application should give a full description of the proposed research, the type of help required (equipment, travel, assistance, etc.), the amount of money desired, and the background and training of the applicant. With young men or women just starting their careers, a supporting letter from one or more recognized ornithologists would be helpful.

Applications should be submitted not later than June 1, 1961, to S. C. Kendeigh, Vivarium Building, University of Illinois, Wright and Healey Sts., Champaign, Illinois.

Programs of divisional meetings of the Cooper Ornithological Society in the latter part of 1960 included the following: in Berkeley, Daniel C. Wilhoft, "A Biological 'Walkabout' in Australia," October 6; L. Richard Mewaldt and Martin L. Morton, "Comparative Reactions of Migratory and Non-migratory White-crowned Sparrows to Like Environmental Conditions," November 3; Richard T. Holmes, "Some Observations on Birds of the Pribilof Islands, Alaska," December 1.

In Los Angeles: Steve F. Briggs, "Birds of Southern Florida" and "Gannets of the Gaspe Peninsula," September 28; Kenneth C. Parkes, "Hybridization Between Different Genera of Birds, with Special Reference to the Manakins," October 26; M. Dale Arvey, "The Status of Ornithology in Colombia," November 30.

Officers of the Southern Division of the Society for 1961 are: M. Dale Arvey, President; Don Bleitz, First Vice-president; Herbert Friedmann, Second Vice-president; N. E. Collias, Secretary. For the Northern Division: Howard L. Cogswell, President; L. Richard Mewaldt, First Vice-president; Robert I. Bowman, Second Vice-president; Ned K. Johnson, Secretary.

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Articles published in the Condor normally are written by members of the Cooper Ornithological Society. Practically all the Society's money goes into the journal; neither the editor nor the business manager receives any pay other than the satisfaction of doing a service worthily. The preparation of good copy by the author will contribute greatly to accuracy of published output, dispatch in handling, and economy of production.

To be acceptable for inclusion in the Condor, articles should contain original material and indicate its significance. They must not duplicate in any substantial way material that is published elsewhere. Any type of subject bearing on birds will be considered. Manuscripts should be sent to the editor at the Museum of Vertebrate Zoology. Proofs with edited manuscripts will be sent to authors, at which time reprints may be ordered.

In the interests of accuracy and economy, observe the following: do not duplicate data in text, tables, or charts; check citations to original sources and verify text references; quoted statements must be exact replicas of the original; use vernacular names applicable to the entire avian species (for a guide in this regard, consult the A.O.U. Check-list of North American Birds, Fifth Edition, 1957; insert scientific names for species but not the subspecific name except in taxonomic papers or where the race concerned has been critically determined by the author or his collaborators on the basis of specimens; revise the manuscript repeatedly to remove superfluous words and phrases, immaterial detail, and repetitious statements.

Note Condor style and usage. "General Articles" and the "Field and Study" items are set up in different form. Provide a concise, meaningful title, and, where needed, subtitles within the text. Footnotes are not used. The address line may serve to indicate institutional connection, and to it should be added the date of transmittal of the manuscript. Terminal bibliographies are usually desirable where five or more titles are to be cited; otherwise, the references may be included in the text. For bibliographic style, note closely the practices employed in recent volumes of the journal. A factual summary is recommended for longer papers.

Rules for copy.—(1) Typewrite material, using one side of paper only; (2) double space all material and leave liberal margins; (3) use $8\frac{1}{2} \times 11$ inch paper of standard weight (avoid onion skin); (4) carbon copies are not acceptable; (5) place tables on separate pages and plan them to fit normal page width; (6) number pages in upper right hand corner.

Illustrations.—Photographs should be glossy prints of good contrast. Make line drawings with India ink; plan linework and lettering for at least $\frac{1}{2}$ reduction; do not use typewritten labels on the face of the drawing. Provide typed legends on separate sheets.

Helpful references on writing: Manual of Style, University of Chicago Press, and Rules of the Editorial Committee, University of California Press. On scientific nomenclature: Fifth Edition of the A.O.U. Check-list, The Distribution of the Birds of California (Pac. Coast Avif. No. 27), and The Distributional Check-list of the Birds of México, Parts I and II (Pac. Coast Avif. Nos. 29 and 33); authors are not required to follow the nomenclature of these works.